

1112-2

# THE AMERICAN NATURALIST

Vol. LII.

January, 1918

No. 613

## INHERITANCE OF NUMBER OF FEATHERS OF THE FANTAIL PIGEON

PROFESSOR T. H. MORGAN

COLUMBIA UNIVERSITY

SEVERAL years ago I began to study the inheritance of the number of the tail feathers in fantail pigeons, partly because of a challenge that I would not recover the fantail in the  $F_2$  generation, the implication being that the inheritance was not Mendelian. The race of fantails is a very old one and the pigeons have been very intensively selected by fanciers for many years. It was therefore to be expected that several modifications had in time been accumulated in the direction of selection. Nevertheless, it was to be expected that if a sufficient number of individuals were bred, the original type would reappear. If two factors in homozygous condition are essential for the reappearance in  $F_2$  of the original fantail, then such an individual is expected once in sixteen cases; if three factors, once in sixty-four cases; if four, once in two hundred and fifty-six; if five, only once in 1,048 cases, etc. This relation holds if the fantail factors are all recessive, but fewer factors are called for if one or more of them is dominant, and the question will be still more complicated if the highest reaches of the variation are due to modifying factors acting only in the presence of other factors.

It seemed unlikely, however, that the situation would be found to be as simple as this; for, in the first place, there is no fixed number of tail feathers characteristic of

27 Jan 19 Binding 1.25

the fantail; selection of these birds has not been made exclusively in regard to number of feathers, but in regard also to their size and shape, their regularity of distribution, their method of spreading, etc. It was a priori unlikely that the race itself is homozygous for *all* of the factors that influence the number of feathers. How far the results would depend on whether the maximum effects are produced by a homozygous condition in several of the factors, with heterozygous condition in others, would be a point not easy to ascertain in a race that produces as few offspring as does the pigeon. Nevertheless, the results give, I believe, pretty clear indications that the effects are due to several factors, and they indicate, moreover, that the failure to recover the extreme type of the fantail in  $F_2$  is probably only a question of insufficient numbers—in fact, the fantail type has probably reappeared in  $F_2$ , though not in its most extreme form, even with the relatively few  $F_2$  pigeons that I have been able to get.

The work has extended over several years, owing to lack of suitable quarters in which to keep the birds and of assistance to take care of them. They had to be removed to and from Woods Hole each year, with the consequent loss of young and disturbance of the regularity of habits essential to a bird as conventional as the pigeon.

The original stock was obtained from Dr. F. D. Solley, of New York City, a well-known breeder of high-grade fantails. Dr. Solley has also supplied me with information as to the number of tail feathers in birds of his strain. Unfortunately these numbers were not obtained until a year after these particular birds had passed out of his hands. He assures me they are typical, and the birds of his stock that I saw when my parent birds were obtained were closely similar in tail number, etc., to those here recorded.

The birds with which the original fantails were bred to get  $F_1$  stock were ordinary birds. As they were not pedigreed stock there is a small chance that they might have contained factors of the fantail type, but this is

highly improbable, since they had the number of feathers characteristic of nearly all other strains of pigeons, and especially of the more common ones.<sup>1</sup> Three  $P_1$  pairs were used (two male fantail and one female) but the  $F_1$  individuals were not kept apart (for want of space) and, as no marked difference appeared amongst the  $F_1$  progeny when the fantail parent was female or male, the  $F_1$ 's from the reciprocal crosses were mixed together. This is unfortunate, for fuller and more accurate observations might have revealed significant differences indicative of sex-linked factors. I can only state that if such are here involved their effect is slight, and was not observed at the time when the two kinds of  $F_1$  offspring were reared.

#### HISTORY OF THE FANTAIL RACE

In his book on "Animals and Plants under Domestication" Darwin has given a great deal of important information about the origin and characteristics of the fantail.

"The normal number of tail feathers in the genus *Columba* is 12; but fantails have from only 12 (as has been asserted) up to, according to MM. Boitard and Corbie, 42. I have counted in one of my own birds 33, and at Calcutta Mr. Blyth has counted in an *imperfect* tail 34 feathers. In Madras, as I am informed by Sir W. Elliot, 32 is the standard number; but in England number is much less valued than the position and expansion of the tail. The feathers are arranged in an irregular double row; their permanent fan-like expansion and their upward direction are more remarkable characters than their increased number. The tail is capable of the same movements as in other pigeons and can be depressed so as to sweep the ground. It arises from a more expanded basis than in other pigeons; and in three skeletons there were one or two extra coccygeal vertebræ. I have examined many specimens of various colors from different countries, and there was no trace of the oil gland; this is a curious case of abortion.<sup>2</sup> The neck is thin and bowed backwards. The breast is broad and protuberant. The feet are

<sup>1</sup> At least one other of the domesticated races may have more than twelve feathers in the tail.

<sup>2</sup> "This gland occurs in most birds; but Nitzsch (in his 'Pterylographie,' 1840, p. 55) states that it is absent in two species of *Columba*, in several species of *Psittacus*, in some species of *Otis*, and in most or all birds of the Ostrich family. It can hardly be an accidental occurrence that the two species of *Columba* which are destitute of an oil gland have an unusual number of tail feathers, namely 16, and in this respect resemble fantails."

small. The carriage of the bird is very different from that of other pigeons; in good birds the head touches the tail feathers, which consequently often become crumpled. They habitually tremble much; and their necks have an extraordinarily, apparently convulsive, backward and forward movement. Good birds walk in a singular manner, as if their small feet were stiff. Owing to their large tails, they fly badly on a windy day. The dark-colored varieties are generally larger than white fantails."

"Mr. Swinhoe sent me from Amoy, in China, the skin of a fantail belonging to a breed known to have been imported from Java. It was colored in a peculiar manner, unlike any European fantail; and, for a fantail, had a remarkably short beak. Although a good bird of the kind, it had only 14 tail feathers; but Mr. Swinhoe has counted in others of this breed from 18 to 24 tail feathers. From a rough sketch sent to me, it is evident that the tail is not so much expanded or so much upraised as in even second-rate European fantails. The bird shakes its neck like our fantails. It had a well-developed oil gland. Fantails were known in India, as we shall hereafter see, before the year 1600; and we may suspect that in the Java fantail we see the breed in its earlier and less improved condition." Vol. I, Chap. V, p. 153.

"The first notice of the existence of this breed is in India, before the year 1600, as given in the "Ayeen Akabery"; at this date, judging from Aldrovandi, the breed was unknown in Europe. In 1677, Willughby speaks of a fantail with 26 tail feathers; in 1735, Moore saw one with 36 tail feathers; and in 1824, MM. Boitard and Corbie assert that in France birds can easily be found with 42 tail feathers. In England, the number of the tail feathers is not at present so much regarded as their upward direction and expansion. The general carriage of the bird is likewise now much valued. The old descriptions do not suffice to show whether in these latter respects there has been much improvement; but if fantails with their heads and tails touching had formerly existed, as at the present time, the fact would almost certainly have been noticed. The fantails which are now found in India probably show the state of the race, as far as carriage is concerned, at the date of their introduction into Europe; and some, said to have been brought from Calcutta, which I kept alive, were in a marked manner inferior to our exhibition birds. The Java fantail shows the same difference in carriage; and although Mr. Swinhoe has counted 18 and 24 tail feathers in his birds, a first-rate specimen sent to me had only 14 tail feathers.<sup>3</sup>

A later statement in regard to fantails from Fulton's Book of Pigeons gives some additional details.<sup>4</sup>

<sup>3</sup> Darwin, "Animals and Plants," Chapter VII, p. 218.

<sup>4</sup> "The Illustrated Book of Pigeons with Standards for Judging," by Robert Fulton, edited by L. Wright. Cassell & Co., Ltd., New York.

The tail also is peculiar, and quite uncommon. It is long and composed of 14 to 22 feathers, 16 being about the average number in these birds; these are arranged equally on either side, one above another, and the two top ones, diverging a little outwards, show a slight division in the tail, but there is not the slightest affinity or resemblance to a "fan" tail, as some might suppose by the excessive number of feathers, but it is a distinct peculiarity of this breed (12 being the normal number of tail-quills in most pigeons). The greater the number of quills in "Oriental Rollers" the more the specimens are valued. A further singular feature noticeable in the tails of these birds is that occasionally two feathers may be found growing from one quill, separating at its pithy junction as a twin feather, each rather narrower than ordinarily, but of the usual length, and not outgrown, or causing a disordered formation of the tail (p. 195).

... The tail is the other chief point in the English breed. The feathers should lie flat and evenly over one another (none of them being set edgeways), so as to form a neat double row. In number they should not be less than 28, but as many more as the bird can carry nicely. The Birmingham Columbarian Society, in an article published by them some years ago, laid down 40, arranged in 3 rows, as the proper number; but though I have heard of such birds I have never seen one. I once had a hen with 38 tail-feathers. I purchased her from Mr. Fulton, and I believe she had been imported from India; and I have often bred birds with tails of 36 or 37 feathers carried in most orthodox fashion. In an exhibition pen the number is of no consequence, provided that the tail is well spread and circular, and well filled up all around; but in the breeding pen a thickly-feathered tail is of great value. In the breeding of any animal for any fancy point, if you can get that point in excess in either of the parents so much the easier is your task. You have then something to *spare*, instead of something to breed up to, which is a very different matter (p. 329).

#### THE P<sub>1</sub> GENERATION

The three original fantails had 29, 30 and 32 tail feathers, respectively (Fig. 1). From Dr. F. D. Solley I got the records of other fantails of the same stock given in Fig. 2. The other parents were ordinary homers purchased from a breeder of these birds.

#### THE F<sub>1</sub> OFFSPRING

The numbers of tail feathers shown by the 41 individuals of the F<sub>1</sub> generation are recorded in Fig. 3. The range of variation is from 12 to 20, with the highest fre-

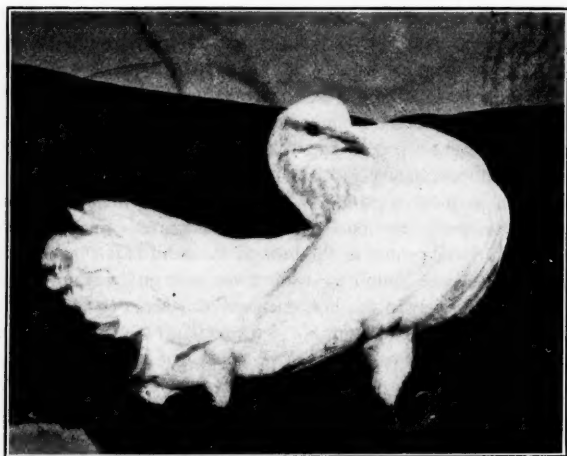
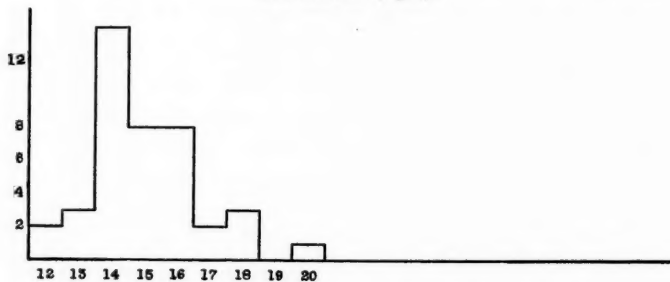


FIG. 1. One of fantail pigeons used in the experiments.

quency in the 14-tail-feather class. Evidently one or more of the factors of the fantail act as partial dominants, producing tails that have for the most part more tail feathers than has the common pigeon but less than the fantail. In appearance these  $F_1$  birds are more like the common pigeon, having lost the peculiar carriage



FIG. 2. Frequency distribution of tail feathers in parent "homers" (left), and fantails (right).

FIG. 3. Frequency distribution of tail feathers in  $F_1$ .

of the fantail and its peculiar shape. The tail is, however, often wedge-shaped instead of flat as in ordinary birds. There were 28 birds with an even number of

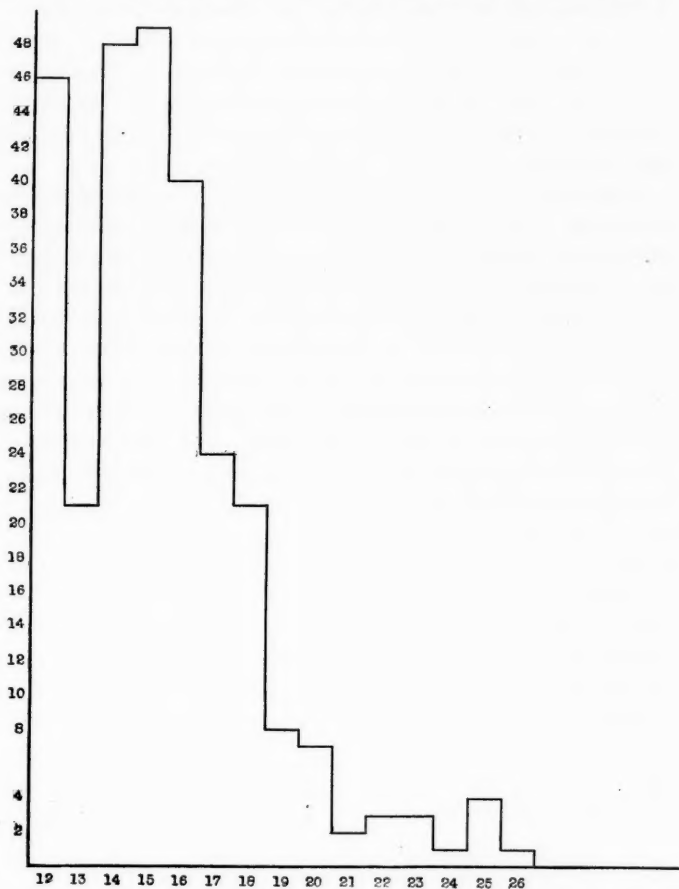


FIG. 4. Frequency distribution of tail feathers in  $F_2$ .

feathers and 13 with an odd number—a considerable preponderance of even number of feathers. Of the 41 individuals, 30 are included in the classes with 14, 15, 16 tail feathers.

THE  $F_2$  GENERATION<sup>5</sup>

A glance at Fig. 4 shows that the range of variation of the  $F_2$  group is greater than that of the  $F_1$ ; that the 12-feathered tail has reappeared in considerable numbers; that the "curve" is at least bimodal with one apex in the 14, 15, 16 rows, and the other in the 12 row; that there are a few individuals that approach the lower range of variation of the fantail, viz., those with 24, 25 and 26 tail feathers.

There is a distinct return of one of the grandparental types, viz., the 12 class. The 13-16 groups clearly correspond to a large part of the heterozygous group seen in  $F_1$ . Whether the range to the right of this middle group in the  $F_2$ 's is significantly different from that in the  $F_1$  can not be determined by inspection, as the number of individuals is too small. If the  $F_1$  and the  $F_2$  groups are made into curves the results show that it is doubtful if the wider range in  $F_2$  is significant, although the large 12-feathered class in  $F_2$  makes the  $F_2$  variability much more marked than the variability in  $F_1$ .

## BACK CROSS

Some of the  $F_1$  birds, both males and females, were back-crossed to fantails. Twenty-three offspring were obtained which differed strikingly as a group from the  $F_1$  and  $F_2$  lots. The number of tail feathers (Fig. 5) was greater; no 12-feathered birds appeared (the lowest num-

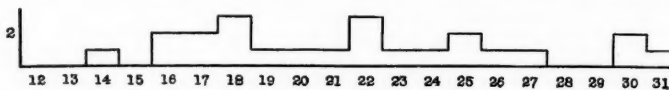


FIG. 5. Frequency distribution of tail feathers in back-cross.

ber was 14); while the highest number included birds with 30 and 31 tail feathers. The latter would undoubtedly pass-for-fantail, so far as the number of tail feathers was

<sup>5</sup> There are some discrepancies between the  $F_2$  and back-cross tables given here and the records of the groups given in "The Mechanism of Mendelian Heredity." The present account is more accurate, as some of the former data was obtained from the birds while still alive.



concerned. The carriage of most of the birds was noticeably much more like the fantail than that of the  $F_1$  and  $F_2$  birds.

#### NUMBER OF FACTORS INVOLVED

The recovery of a certain number of the normal 12-feathered tail in the  $F_2$  might seem to furnish a basis on which to calculate the number of factors involved; but the fact that a few 12-feathered birds appear in  $F_1$  shows that some, at least, of the heterozygous combination are included in the  $F_2$  twelve feather group. It is also possible, even probable, that other  $F_2$  combinations may also fall within this group. It is impossible, therefore, to arrive at anything more than a possible conclusion from the  $F_2$  data because the relative value of the heterozygous classes can only be guessed at.

Two factors will obviously not fit the results, because there would be expected more of the higher numbers of tail feathers both in the back cross and in the  $F_2$  count. Three factors fit fairly well. Let A, B, C represent partially dominant factors for fantails, and a, b, c their normal allelomorphs (aabbcc being the normal 12-feathered tail). In the  $F_2$  there will be expected only one pure fantail out of 64 (viz., AABBCc) and one pure 12-feathered type (viz., aabbcc). There will be six  $F_2$  classes with only one dominant factor heterozygous for A or B or C. These, theoretically at least, if all the factors have equal efficiency, would be the most likely ones to fall within the 12-feathered group. If these include all of the expected 12-feathered tails in  $F_2$  there should be seven 12-feathered in 64. There were 278  $F_2$  individuals. On the same calculation this would give an expectation of only 10.5 twelve-feathered tails. But the  $F_2$  records actually gave 46 normal tails. Obviously still other combinations realized in  $F_2$  must come under this class. It would be mere guesswork to try to state which are the more probable combinations.

The back cross furnishes data that permit a better means of calculation. Here eight kinds of germ cells and eight

zygotes are expected on the assumption of a three-factor cross, viz.,

ABC	ABc	Abc	aBC	abC	aBc	abc
abc	abc	abc	abc	abc	abc	abc

Of these eight kinds of individuals, some of only one class, might be expected to be wild type (viz., of class abcABC) in the sense that individuals of this class correspond in formula to the  $F_1$  offspring, and, of these  $F_1$  offspring, 2 out of 41 have tails with 12 feathers, or 1 in 20. Amongst the 24 back crossed individuals, there were none with 12 feathers only and at most one is expected. If we assign to the group of abcABC also the four individuals of the back cross in the 14 and 16 groups, and assign the 3 individuals of the 30 and 31 groups to the pure fantails, there remain 17 individuals in the middle range that belong to the six intermediate groups that are homozygous in one or in two fantail modifiers. There are six intermediate classes between the end classes just spoken of. If we are right in the limits assigned to the end classes, the expectation would be 18 individuals for the intermediate classes, where 17 are so classified, which is also not a bad fit.

Four factors fit the data about as well as three,<sup>6</sup> but if three will suffice the smaller number is perhaps preferable. It is evident that the data do not allow close analysis, but only because they are not sufficiently large, especially in the back cross. Nevertheless, it is important to find out that, so far as the results go, they are not unconformable with the Mendelian assumption of segregation of a few pairs of factors.

#### LINKAGE

When all  $F_2$  tails that are blue are classified they fall into the groups shown in Fig. 6; similarly, the white tails

<sup>6</sup> On this assumption relatively fewer fantails are expected in  $F_2$ , which is a better fit, but fewer also in the back cross, which apparently is not so good a fit. The proportion would also depend, however, on the relative efficiency and the completeness of the dominance of each factor. The above evidence proves that there must be at least three factors.

give the groups shown in Fig. 7. A comparison of these groups shows that there is a relatively large number of high-feathered tails amongst the whites, while among the

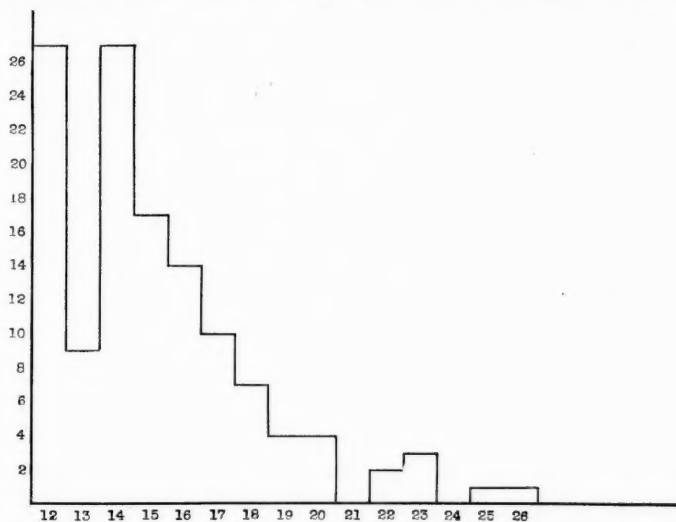


FIG. 6. Frequency distribution of blue tail feathers in  $F_2$ .

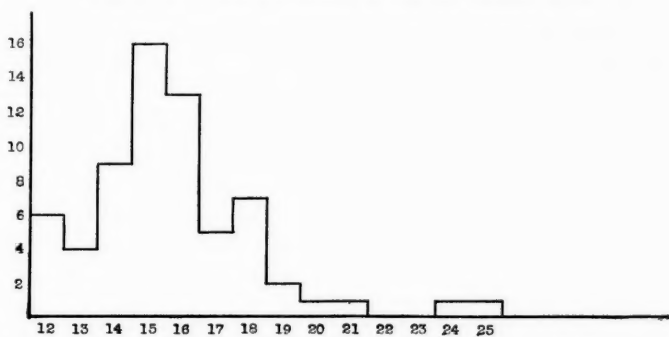


FIG. 7. Frequency distribution of white tail feathers in  $F_2$ .

blues, the 12-feathered tails are relatively more frequent. A not improbable interpretation of this relation is that the principal factor for white is linked to one or more of the factors for increased number of feathers.

Since these results occur in the  $F_2$  count, it is unfortunately not possible to deduce from them whether crossing over takes place in one or both or neither sex.

Amongst the tails were some that had both blue feathers and white feathers. These give the group shown in Fig. 8, which closely corresponds to the blue-tail group (Fig. 6). There were other tails with white feathers having

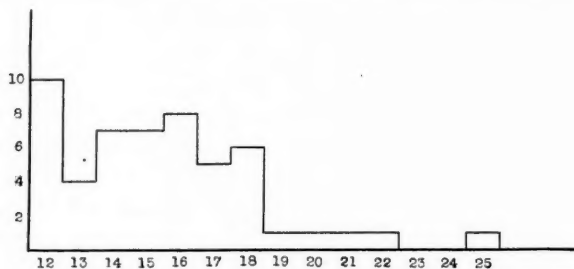


FIG. 8. Frequency distribution of blue-and-white tail feathers in  $F_2$ .

pigment along the margins as in Fig. 15. These, when classified, gave the group shown in Fig. 9, which apparently is the same as the group of white tails (Fig. 7).

The number of birds in the  $F_1$  and in the back cross are too few to give significant results when broken up into the two groups of white or blue.

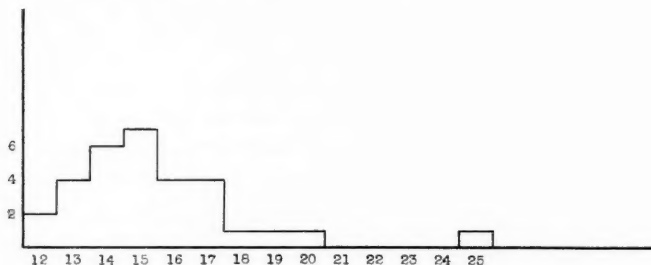


FIG. 9. Frequency distribution of "edged white" tail feathers in  $F_2$ .

The tails are not a complete index of the bird from which they came, for a bird with a pure white tail might have color patches elsewhere on its body; but as no rec-

ords were kept of the entire color of each bird, it is not now possible to find out how closely the complete pattern would correspond with the tail color. In general, however, in these birds the tail is a partial index, at least—a fair sample, perhaps—of the entire color.

“CORRELATION” BETWEEN THE OIL GLAND AND THE NUMBER  
OF TAIL FEATHERS

Darwin suggests a “correlation” between the absence of the oil gland and the increased number of tail feathers. Such a relation might be a direct correlation in the sense that the overdevelopment of the tail feathers suppresses or tends to suppress the development of the oil gland that is situated on the uropygium just above the base of the tail feathers. If this were the true interpretation of the condition in the fantail, one would expect to find in  $F_1$  and  $F_2$  all degrees of development of the oil gland. If, on the other hand, the absence of the oil gland is an inherited peculiarity having nothing directly to do with the number of feathers, then in the  $F_2$  series we might expect to find a numerical relation indicating its mode of inheritance. Unfortunately the pedigrees of the normal tailed pigeons that had been mated to the fantails were unknown. While the oil glands may be occasionally absent in domesticated pigeons, it is highly improbable that any of the homers used in the experiment carried such a factor. In classifying the  $F_1$  and  $F_2$  birds according to the condition of the oil gland three classes were recognized. First, “double” glands, those with the right and left sides almost separate, each with a separate opening; second, “single” glands, those with the halves united more closely and with but one external outlet;<sup>7</sup> third, those with no oil glands. The results are given in graphs of Figs. 10–11.

The few  $F_1$  birds available when the oil gland was studied show a wide range of variability; all but one were double, Fig. 10 (above). This doubling might be due to

<sup>7</sup> An intermediate stage was also noted, viz., one with two closely fused so as to make almost a single gland.

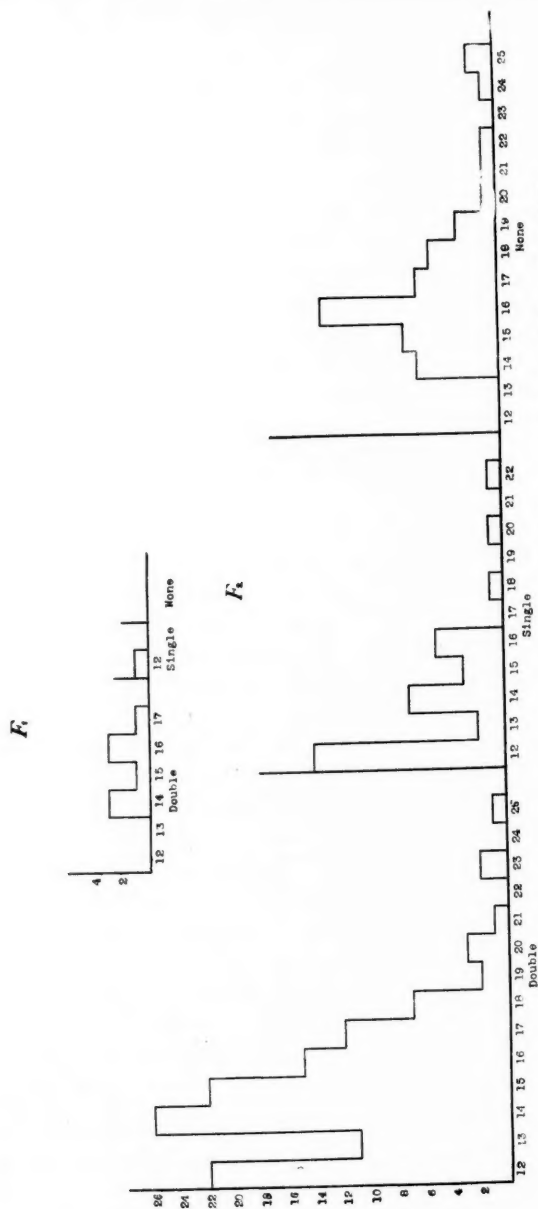


FIG. 10 (above). FIG. 11 (below). Frequency curves of occurrence of oil glands in  $F_1$  and  $F_2$ .

partial dominance of a gene for doubling, or to a "correlation" such as Darwin spoke of, for the number of tail

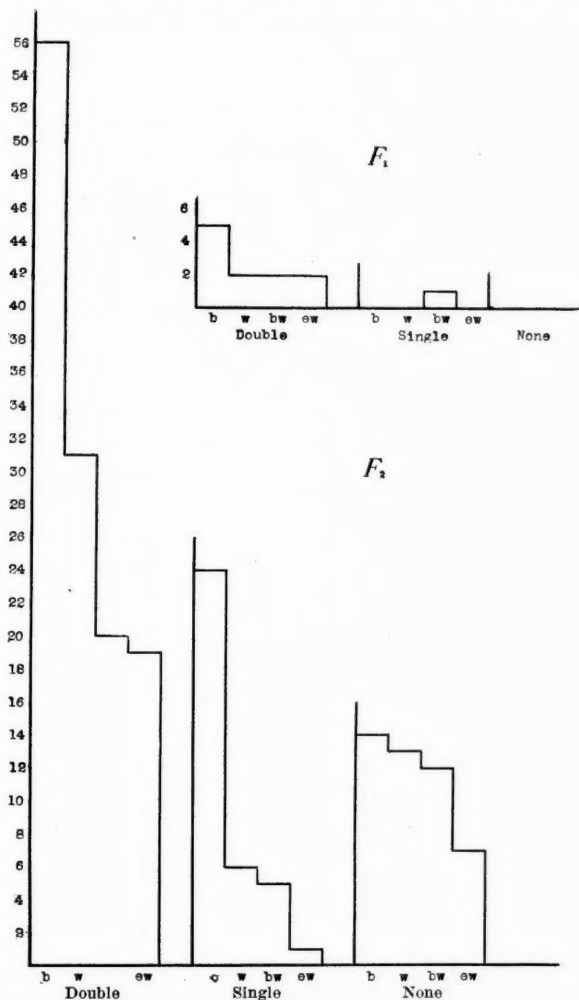


FIG. 12 (above). FIG. 13 (below). Frequency distribution of double, single and no oil glands in differently colored tails.

feathers in this particular lot was high. That the latter is probably not the explanation is shown in the  $F_2$  birds.

The three groups of  $F_2$  tails (Fig. 11) show 126 doubles, 36 singles, 46 none. The expectation for two factors (9:3:4), on the assumption that the doubles differ from the singles by one factor, and both from none by another factor, is 117 doubles, 39 singles, 52 none. This is not a very bad fit.

There is one striking result brought out by these curves. There are no 12- or 13-feathered birds without an oil gland. This is an expression of the relation that Darwin suggested as due to "correlation" in the sense that more tail feathers suppressed the development of the oil gland. But there is no such obvious solution as is shown by the  $F_2$  group, for there may be a large number of tail feathers present and the oil glands be well developed, single or double. The curves suggest, rather, linkage between a gene for extra feathers, and a gene for absence of oil glands.

The tails with double, single and no oil glands were also classified according to the four color groups already referred to, viz., blue, white, blue and white, edged white (Figs. 12 and 13). The double and single curves appear to be the same, the no oil gland curve seems significantly different. If so, it means that there is some linkage between white color and absence of oil glands.

The foregoing evidence makes probable the view that a gene for more than 12 feathers, and the gene for no oil gland, and a gene for white color are linked, *i. e.*, are carried by the same chromosome. The genes for the oil gland and for the number of tail feathers are closer to each other than either is to the gene for white. More data, especially from back-crosses, will be necessary to establish this conclusion.

#### SPLIT FEATHERS

Dr. Solley tells me that the split and double feather that occurs at times in the fantails is selected against. It is of not infrequent occurrence in the  $F_2$  and back-crossed birds that I have obtained. In the records these



split feathers have been counted as *one* feather, without, however, intending to prejudice the question of the single or double nature of these feathers.

The most striking cases are like those represented in Fig. 14 (top row) and Fig. 15, where what appears to be

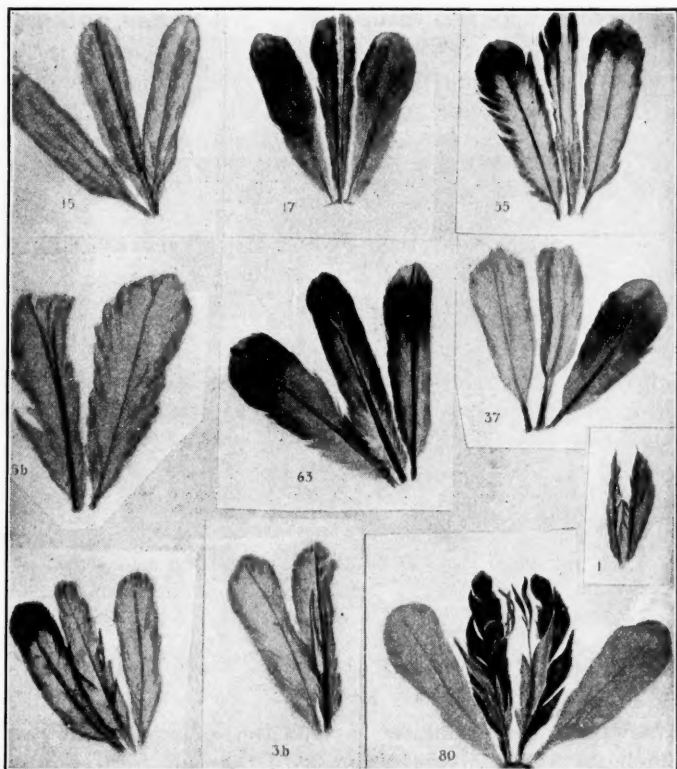


FIG. 14. Some types of split feathers.

a single feather is split in two throughout its length. While there may be a complete shaft in each half, yet the two vanes that lie on the "inner" side are not so broad as the outer half vanes, and their edges are generally frayed out and imperfectly formed. Often the vanes run across and unite the two halves.

In some of the split feathers, the division is obviously into right and left halves (Figs. 14, 15, 16); in other cases the halves make an angle with each other (Fig. 14, Nos. 37 and 80), while in still others one larger part may lie above a smaller part (Fig. 14, lowest row). Whether in the last cases the division has been in a horizontal plane, and in the first cases in a vertical one, is not certain, although the shape of the feathers even in the last case, with the imperfect edge and a narrower margin, would seem to make most probable the view that in all cases the division

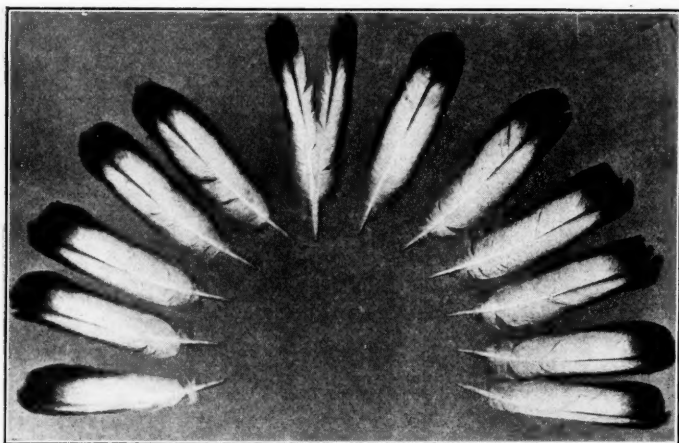


FIG. 15. An  $F_2$  tail ("edged white") with one split feather.

has been into morphological right and left halves. The final position of the feather halves may be due to a later twisting in the sheath, or to crowding of the feathers at the base. This interpretation is further substantiated by cases in which the center of all the feathers has a white area (Fig. 14, No. 55, and Fig. 15); this is found on the imperfect side of the split feathers even when they lie one above the other. In all there were 24  $F_2$  tails with split feathers. Five of these had each two split feathers.

These cases grade into those in which only the distal end of the feather is split, as shown in Fig. 14, middle figure, and Fig. 16. The impression produced by feathers

of this kind is strikingly in favor of a single feather split into right and left parts at the distal end. In all, three cases of this sort were found.

To the same group are to be referred two cases, one of which is shown in Fig. 14, No. 5, *b*. Here there is a single feather, but the midrib is split near the end. The vane

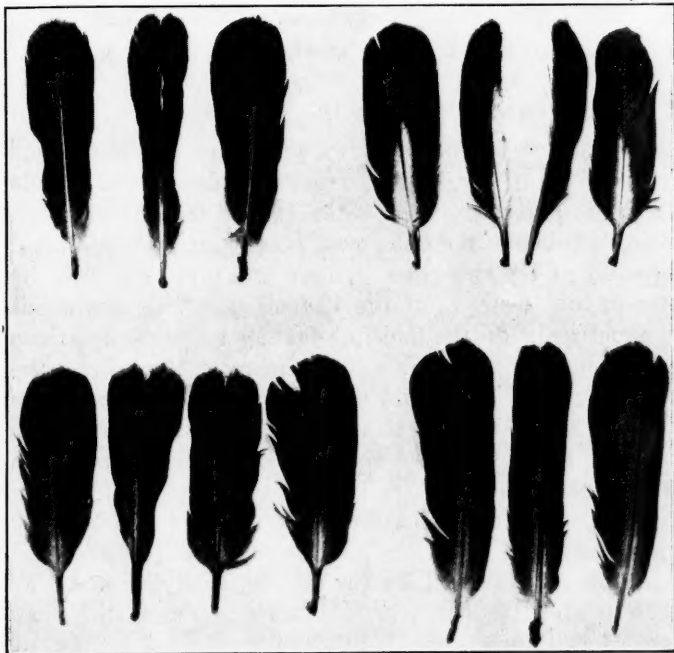


FIG. 16. Split feathers with normal feathers that lie next to them.

lying between the two midribs is continuous, yet the bending inwards of this part is indicative of its dual nature.

More extreme are the eight cases of which three are shown in Fig. 16, lowest row. In all such cases there is a large, almost fully formed feather with a smaller, less perfect piece *underneath* the larger part. The first impression is that a piece has been split off the ventral side of the feather by a division in the horizontal plane. A

closer scrutiny shows, however, that the large feather is ragged along one edge only (or on a part of one edge), while the smaller piece has also on the same side (as can be seen in some cases at least) a ragged edge with the other vane more nearly complete and with a not-rough edge. It seems, therefore, more reasonable to interpret even these cases as extremes of the split-feather type in which one piece has fared worse than the other (or in which the original division was into unequal pieces).

#### THE SIZE OF THE DOUBLE FEATHERS

There is a graded difference between the outer and inner vanes of the feather from the edge to the middle of the tail Fig. 15. The outer half of the vane is relatively smaller in the outermost feather, right or left, and equality of the two sides is more and more reached, the two middle feathers of the 12-feathered tails are about symmetrical. In the multiple feather tail these relations still hold, but are more difficult to trace than when the tail is simpler. It would not be profitable to attempt to analyze in detail these relations as applied to the double feathers further than to compare their surface relations with that of the feathers nearest to them or with their symmetrical mates. In all cases of split feathers the outer halves of the vanes are not so wide as is expected from the nearest feathers (or their symmetrical mates as seen in Figs. 14-16). The middle part is, as a rule, very much less than a right or left vane. The total width of the split feather is, as nearly as I can judge, about the same as the expected feathers for that position. The impression indicates that the sum of the four vanes is a little greater than the sum of the two normal vanes, but there can not be much difference as measurements show. The looseness of the frayed inner edge makes it difficult to get a very close estimate of the actual relations.

The general conclusion is that we are dealing with a single rudiment that has split at a very early stage into two parts that have completed themselves as whole

feathers, so far as this intimate union in the middle line of the bud permitted. There are no indications that the split feather is due to the union of two separate rudiments that have been pressed together so closely as to interfere with the full development of each when they came in contact.

## THE LOCATION OF THE SPLIT FEATHERS

The location of the split feathers (and modified types) is given in the next table.

Feather “split” ...9 near middle, 1 one quarter from side

End only split . . . . . 2 near middle, 1 one third from side

Double vein at tip. . 2 near middle

Very unequal parts. 7 near middle,  $\begin{cases} 1 \text{ two thirds from side,} \\ 1 \text{ outermost feather.} \end{cases}$

In the great majority of cases the doubling occurs near the middle of the tail. The meaning of this is not at all apparent. We know so little about the cause of duplication in general and about the embryological mechanism that is involved in laying down the feathers in the tail, that it is useless to speculate about the result. The evidence from experimental embryology shows unmistakably that doubling may result from a mechanical interference with the relation of the blastomeres after they have assumed a definite position in regard to each other, but there are also many other cases known where, in normal development, a part is repeated several or many times. In these cases we can as yet only surmise that the rudiments of the structure—simple cells or groups of cells—become mechanically drawn apart by the more rapid growth of surrounding parts and separated so that each gives rise to a separate organ. Split feathers, from this point of view, would be looked upon as an incomplete separation of certain of the rudiments. However this may be, one can imagine other ways by which a specialized group of cells could become broken up into islands.

## OTHER CHARACTERS IN THE CROSS

Three other characters are conspicuously present in the fantails besides the tail, viz., the white plumage, the carriage of the bird, and the shaking of the head and neck. The dominance—incomplete—of the white of the fantail was noted,<sup>s</sup> but the mixtures that appeared both in  $F_1$  and  $F_2$  make it probable that the results are not due to a single factor. The extraordinary position of the fantail pigeon with its head thrown back until it touches the tail feathers appears also to be due to at least as many factors as is the number of feathers in the tail; for it was not recovered in any of the  $F_2$  birds, although in the back cross there were birds that showed some approach to the fantail posture. The shaking of the head disappeared in  $F_1$  and indications of it were seen occasionally in  $F_2$  and especially in back crosses. The character is of such a kind that its study is difficult, and it may well be an expression of some structural modification of the body rather than any direct psychological factor.

## CASTRATION OF MALE

The absence of marked secondary sexual characters in the male, characters that are so conspicuous in many other birds, suggested the possibility that here, as in the Sebright male fowl, the suppression of the male plumage might be due to substances developing in the testes. Unlikely as this seemed (because pigeons with diseased testes would probably have occurred and any change recorded), nevertheless I tried the effect of castration on one young  $F_2$  male that was just weaned. Some feathers were removed at the same time. The bird was kept for about five months and did not show any change in its plumage. It appears probable, then, that there are no genetic factors in pigeons, like those in the Sebright, which, acting through the testes, suppress the development of the plumage in the male.

<sup>s</sup> See Cole *et al.*

## REFERENCES

- Browne, R. Staples.—On the Inheritance of Color in Domesticated Pigeons with Special Reference to Reversion. *Proc. Zool. Soc. London*, 1908.
- Bonhote, J. L. On the Inheritance of the Webfoot Character in Pigeons. *Proc. Zool. Soc. London*, 1911.
- Bateson, W. Mendel's Principles of Heredity. 1913, p. 36.
- Morgan, T. H. Notes on Two Crosses between Different Races of Pigeons. *Biol. Bull*, XXI. 1911.
- Morgan, T. H., Sturtevant, A. H., Muller, H. J., and Bridges, C. B. The Mechanism of Mendelian Heredity. New York, 1915, p.
- Cole, J. A Case of Sex-linked Inheritance in the Domestic Pigeon. *Science*, XXVI, 1912.
- Darwin, Chas. Animals and Plants under Domestication.

## A PRELIMINARY REPORT ON SOME GENETIC EXPERIMENTS CONCERNING EVOLUTION

RICHARD GOLDSCHMIDT

THE nature of the gene, the variability of factors and the effects of selection are favorite topics of recent discussion, which is well known to geneticists. The latest publications of Jennings and Castle will stir up anew the uncompromising parties and lead to new discussions. We think it advisable, therefore, to give a brief account of certain parts of a very large body of work on fundamental questions of evolution which we have carried on during the past nine years, with the collaboration of Dr. Seiler and Dr. Poppelbaum. Although some parts of the work have been finished for some years, we do not intend to publish a full account until all the details are worked out. But as certain results have already allowed us to form definite views in regard to some fundamental questions of evolution, we may present them, together with examples of the experiments in question.

The majority of the experimental work in regard to the fundamental problems of evolution has been done with domesticated animals and their mutations (rats, *Drosophila*) or with Protozoa, which present the complication of asexual reproduction. We have directed our attention to experimental analysis of such phenomena in nature, which must give basic information about evolution, and we have studied the following phenomena:

1. *The Geographic Variation of the Gypsy-moth.*—This well-defined species is spread over a great part of the globe. In different habitats, however, different races are found. How many of these exist can not be stated, but the number must be extraordinarily large, as we know but two localities where the same race is found. We have found all the races to be perfectly fertile with each other, with the exception of one combination which has never been successful. We have studied and are still studying the genetics of a large number of these races.



2. *The Melanism of the Nun-moth, *Lymantria monacha*.*—The nun is one of the moths which have developed melanic varieties within recent times; and these melanic varieties, which were extreme rarities not many decades ago, have almost supplanted the original white form. We have worked out the genetics of this case and shall publish the details when conditions permit. Some of the results were read before the German Zoological Society in 1911 but no abstract was published.

3. *The Genetics of Alpine Varieties, especially of *Parasemia plantaginis* and the Italian Races of *Callimorpha dominula*.*—This work has been broken off by the war, but some of the first results are available.

We shall begin with a few facts concerning the geographic variation of the gypsy-moth. We have here a form that is spread all over Europe, through Siberia into China, and all over Japan, infesting, furthermore, part

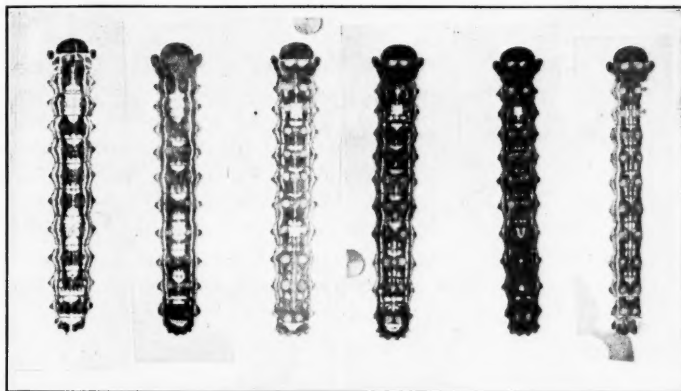


FIG. 1. Types of Caterpillars from different races after the first moult.  
Drawings by Mr. Yokoyama, Tokyo, 1914.

of the Atlantic coast of the United States. We have studied races from different parts of Europe and Japan and the Massachusetts form and we have found different forms in comparatively near-lying regions. Thus the races from the Rhineland, Silesia and Hungary are dif-

ferent from each other and from the Massachusetts race (probably imported from France). All of them are different from the Japanese races and these again differ in the different parts of Japan. The characters of difference are manifold; we shall confine ourselves here to a single character, more interesting and more characteristic than the others—the markings of the caterpillars. Fig. 1 shows caterpillars of a few races after the first moult. We see here some of the transitional stages from a very light to an almost black caterpillar. The genetic study of this character of marking shows that we are dealing here with a primary type of marking which belongs to the entire group of moths in a similar form, that is, the light pattern. All the darker forms have the same genetic basis of marking, on which, however, dark pigment encroaches increasingly until the markings practically disappear. We may now divide this increasing melanism into ten classes and place the lightest individuals in Class X and the ones without marking in Class I. It must be added that the dark series extends beyond Class I, but the difficulty of classifying them is such that no darker classes have been adopted.

The young caterpillars of the different races show markings which fluctuate around a mean at a certain point of the series and this behavior is remarkably constant for the different races. The following Table I gives a few polygons for different European and Japanese races.

TABLE I  
CLASS FREQUENCIES IN PER CENT.

Breed	Race	I	II	III	IV	V	VI	VII	VIII	IX	X
WA3 .....	H	..	..	..	..	..	..	..	38.6	54.5	6.9
UA24 .....	K	..	..	..	..	..	..	15	64.7	20.3	..
UA17 .....	F	..	..	..	..	..	1.5	60	38.5	..	..
VA2 .....	O	..	..	..	..	..	8.2	48.8	31.4	11.6	..
VAS .....	G	..	..	..	..	..	..	11.8	57	31.2	..
WA4 .....	A	..	..	..	..	19	43	38	..	..	..
WA1a .....	S+	..	5.4	19.1	44	30.2	1.3	..	..	..	..
WA56 .....	M, S	100			..	..	..	..	..	..	..

In crosses of these different types  $F_1$  is about intermediate, as some curves in Table II show.<sup>1</sup>

TABLE II  
 $F_1$ . CLASS FREQUENCIES IN PER CENT.

Breed	Cross	I	II	III	IV	V	VI	VII	VIII	IX	X
VA17.....	S × K	..	..	..	..	17.3	29.6	39.9	13.2	..	..
VA18.....	K × S	..	..	..	9.2	33.3	14.4	42.2	0.9	..	..
VA21.....	S × A	..	..	..	..	45.4	28.7	25.9	..	..	..
VA22.....	A × S	9	20	29	11	15	13	3	..	..	..
VA23.....	S × O	..	..	..	4.7	67.4	27.9	..	..	..	..
VA24.....	O × S	..	..	..	..	9.9	66.9	22.4	0.8	..	..
VA37.....	K × H	..	..	..	..	..	0.7	..	49.6	49	0.7
WA83.....	G × M	..	..	2	24	34	32	8	..	..	..
WA88.....	M × A	..	..	..	10	70	20	..	..	..	..

And  $F_2$  gives a 1:2:1 ratio, or 3 light + medium:1 dark, whatever races are involved. (This statement should be taken only on its face value. As a matter of fact, we find here, within the invariably present ratio of 3:1, very strange details of the kind described as "gametic contamination," and, furthermore, an obscuring of the ratio in earlier stages followed later by the right ratio, apparent lack of segregation, etc. From a purely genetic point of view, the analysis of these phenomena constitutes the most interesting part of this work, but it has no special relation to the problems here under discussion.) Back crosses, however, give a 1:1 ratio. The following table gives a few data of this kind.

TABLE III

Breed	$F_2$ From	Dark, Per Cent.	Light + Medium, Per Cent.
WA12.....	S × K	23.8	76.2
WA13a.....	K × S	25.5	74.5
WA24b.....	S × Ky	25.9	74.1
WA28a.....	A × S	25.3	74.7
WA31.....	O × S	26.2	73.8
WA18.....	S × H	30.2	69.8
ZA20.....	O × M	22.1	77.9
ZA9.....	M × H	25.8	74.2
ZA12.....	G × M	25	75

<sup>1</sup> We give here a few random examples. The amount of actual material is very large, as more than 100,000 caterpillars have been bred and studied. We refrain, furthermore, from all such details as behavior in reciprocal crosses, etc.

The actual curves look like the example in Table IV of an  $F_2$  cross.

TABLE IV  
ZA9  $F_2$  FROM  $M \times H$

	I	II	III	IV	V	VI	VII	VIII	IX	X
Individuals.....	24	..	..	..	13	9	29	15	3	..
Per cent.....	25.8	..	..	..	14	9.7	31.2	16.1	3.2	..

The sum of all the hundreds of curves shows that we are dealing here with a case of multiple allelomorphism: The pigment factor, producing the gradual covering of the markings, is present in the different races in different degrees, all being allelomorphic to each other.

Thus far we have dealt only with the very young caterpillars. Their further history in regard to the effect of these factors leads us one important step further. We find mainly the following types of behavior within the pure races: (1) Light marked caterpillars, which remain practically the same throughout the entire larval life. (2) Light-marked caterpillars which grow darker with every moult and finally are about medium or more than medium dark. (3) Light-marked caterpillars which change during the larval stage, so that they finally are all dark. (4) Medium light caterpillars of different degrees changing to dark during larval life. In the following tables we give a few examples of these races, showing the shifting of the type of marking during the stages of larval life. The large range of variation after the third and fourth moult visible in these tables is due more to a different speed of shifting in different individuals than to the initial variability. This is shown in Table VI, which gives an example of the shifting of types of pigmentation during the larval stages for a series of isolated individuals of some of the pure races.

The genetic analysis of this phenomenon seems to reveal the real nature of the multiple allelomorphs, which cause these different types of pigmentation and their behavior during development of the caterpillars. With-

TABLE V  
EXAMPLES OF SHIFTING RACES

*Race H*

Class Frequencies in Per Cent.

Stage of Caterpillars	I	II	III	IV	V	VI	VII	VIII	IX	X
3	..	..	..	..	..	..	..	38.6	54.5	6.9
4	..	..	..	..	..	11.8		55.3	31.7	1.2
5	29.3	24.4	9.7	12.2	9.8	12.2	..	2.4	..	..
6	64	16	16	4	..	..	..	..	..	..

*Race A*

Stage of Caterpillars	I	II	III	IV	V	VI	VII	VIII	IX	X
3	..	..	..	..	19	43	38	..	..	..
4	..	..	..	..	35.5	58.1	6.4	..	..	..
5	14.3	42.9	4.7	9.5	28.6	..	..	..	..	..
6	100			..	..	..	..	..	..	..

*Race G*

Stage of Caterpillars	I	II	III	IV	V	VI	VII	VIII	IX	X
3	..	..	..	..	..	..	11.8	57	31.2	..
4	..	..	..	..	1.4	35.2	33.8	28.2	1.4	..
5	3.6	7.2	14.4	18	25	22.8	9	..	..	..
6	100			..	..	..	..	..	..	..

TABLE VI  
EXAMPLES OF SHIFTING AS OBSERVED IN INDIVIDUALS WITH DIFFERENT  
NUMBER OF MOULTS

Race	Individual	Class of the Individual after Moults					Sex
		2	3	4	5	6	
H	ZA3.6	IX	VII	II			♂
"	ZA3.7	VIII	VII	I			♂
"	ZA3.4	IX	III	I			♂
"	ZA3.1	VIII	VII	I	I		♀
A	ZA4.1	VI	V	III			♂
"	ZA4.3	V	III	I			♂
"	ZA4.4	VI	VI	IV	I		♀
"	ZA4.8	VII	V	III	II		♀
"	ZA4.13	VI	V	IV	I		♀
G	ZA6.11	VIII	VIII	VI	II		♂
"	ZA6.7	VIII	VI	VI	IV		♂
"	ZA6.5	VIII	VIII	VI	III		♀
"	ZA6.6	VIII	VIII	IV	III	I	♀
"	ZA6.17	VIII	VI	V	III	I	♀

out going into details, which would necessitate a multitude of tables and curves being given, the following points

are of importance: (1)  $F_1$  between a non-shifting light race and an always dark race is intermediate, or somewhat lighter in the beginning. But by progressive stages the hybrid caterpillars shift over into the dark classes.

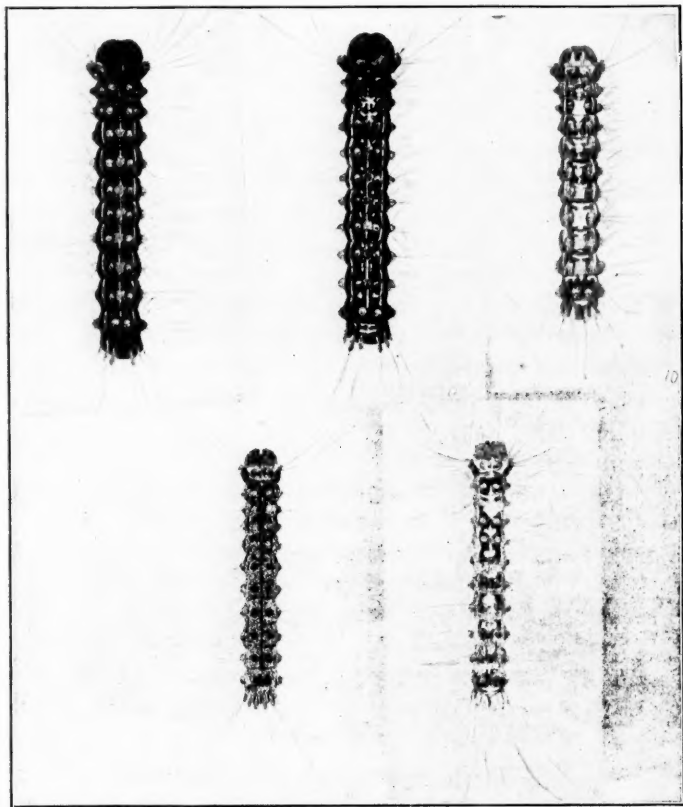


FIG. 2. First row: hybrid between the two parental races after second moult. Second row: Hybrid (left) and light parental race (right) after fourth moult. Drawings by Dr. Poppelbaum, 1912.

Fig. 2 represents caterpillars from a cross of this type. (The exact curves that belong with these pictures are reproduced in our "Einführung in die Vererbungswissenschaft," 2d edition, 1913, p. 170, Fig. 66, as an example

of change in dominance during development.) (2) The same thing happens in certain  $F_2$  crosses, reversing completely during larval life the original ratio of lights and darks. (3) The different races involved are characterized by a difference in the speed of differentiation, as shown in the actual curves. This velocity is also caused by genetic factors. Where these recombine with the pigmentation factors, the entire situation of the  $F_2$  curve is shifted (without changing the 3:1 ratio), showing that the visible effect of the pigmentation factors is bound to a certain velocity of differentiation. (4) The shifting of the type of pigmentation from light to dark during larval life of certain races or hybrids is a process which progresses constantly with time. This is seen when isolated individuals are studied which belong to races that differ in regard to the number of moults and exhibit the shifting simultaneously. There are races where all the male caterpillars have four moults and the females either four or five; other races where the males have four, the females five; others where both sexes have five moults; and in the last case even a sixth moult occasionally occurs. In these cases we see that every new moult produces a further shift to the dark side of the curve, showing that the class of pigmentation to which a full-grown caterpillar belongs is in this case a function of the time of differentiation. The same fact can be demonstrated in a shifting race by prolonging the time between two moults by starvation (which succeeds only to a certain extent). In experiments of this sort it has been possible to get the shifted type of pigmentation, characteristic of the fourth stage, in some individuals in the third stage. Table VI also contains a few random data on the first point. (6) In shifting hybrid cultures there appear comparatively often mosaic-caterpillars, showing different classes of marking on right and left sides. The distance between these two different classes is approximately kept up when shifting occurs during development. The following example demonstrates this fact:

TABLE VII

	Class After Second to Fifth Molt							
	2		3		4		5	
	Right	Left	Right	Left	Right	Left	Right	Left
WA51, 27 .....	IV	III	IV	II	III	I	I	I

These caterpillars always give normal moths and normal offspring.

A careful consideration of these points shows clearly what these multiple allelomorphs for pigmentation really are: They are different quantities of the substance which we call a gene which act according to the mass-law of chemical reactions, *i. e.*, produce a reaction or accelerate it to a velocity in proportion to their quantity. In our special case it means that the factor stands for a metabolic

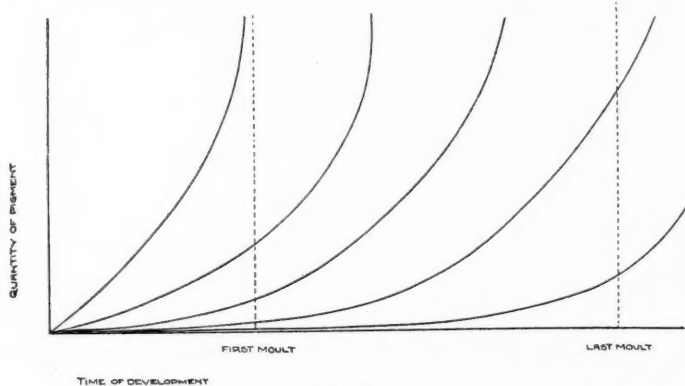


FIG. 3.

activity proceeding with a definite velocity dependent upon the quantity of the factorial substance present. This activity finds its visible expression in the deposition in the skin of increasing quantities of certain products of protein decomposition which as chromogens are oxidized into melanin pigments. The effect of the different quantities of active substance (enzyme?) which we call the multiple allelomorphs upon the progressive pigmentation



of the caterpillars is then represented by the graph on p. 36 (Fig. 3).

Given a definite quantity of the factorial substance and identical conditions, the velocity of the reaction is constant. Thus the final result depends upon the amount of the factorial substance present and the independently inherited rapidity of differentiation, which determines the situation of the growth-stages on the abscissa (the dotted lines). Thus the above quoted facts as well as the multitude of details not mentioned can be easily derived from this graph. The last named mosaics are of course the expression of small differences in the velocity of differentiation in symmetric halves of the body, which are well known to embryologists.

These conclusions in regard to the real character of multiple allelomorphs are the same as those derived from other characters in the same objects. In our work on intersexuality we were able to prove, to as great an extent as a genetic proof can possibly be carried, that the different geographic races of the same moth differ in regard to the absolute and relative quantities of the substances, which we call the sex-factors. In the genetic language of the present day we should call them, therefore, multiple sex-allelomorphs, a conception which indeed we have always used (without this recent term) since our first report about this work in 1911. In the case of intersexuality we can furnish facts very similar to those about the caterpillars, if we consider certain features of the wing colors. In normal males a certain amount of pigment covers the entire wing, whereas the female wing is unpigmented. This pigment is formed by the oxidation of a chromogen deposited within the scales. There it flows from the wing veins with the blood. By a detailed analysis we are able to show that an intersexual male is a genetic male which developed as such up to a certain point when the development suddenly began to continue under the aspects of femaleness. One of the results of male metabolism is the production of these chromogens

in late larval stages. This production is therefore stopped when female metabolism sets in; when then the time arrives in development, when the chromogen spreads over the wing scales, its available amount is proportional to the relative lateness of the reversal of sex. Therefore, with increasing intersexuality, the pigment flowing from the veins covers a smaller and smaller area of the wing, finally being confined to the neighborhood of the veins. As<sup>2</sup> the analysis of the other intersexual organs allows an accurate determination of the time factor involved, we have here a very close physiological parallel to the facts about the caterpillars.

In most other cases of multiple allelomorphism only the results can be seen, and it will be difficult to work out the time factor, which proves that the multiple allelomorphs are different quantities of an active substance. (Some botanical subjects ought, however, to be favorable.) But in comparing the other facts about multiple allelomorphs with our cases, we feel confident that, wherever a similar analysis can be applied, the results will be the same. For example, all the cases of quantitatively different pigmentation, which are of multiple allelomorphic nature, like Castle's hooded rats or our different cases of melanism in moths, show that the effect of the different factors is that different quantities of pigment spread from different "points of outlet," which of course are hereditary traits of the species or group; the similar effect, therefore, leads to suspect a similar cause.

If our conclusions regarding the nature of multiple allelomorphs are accepted, it must lead to a different intellectual attitude toward the problem of variability of genes, which is so important for evolution. The opposition to the view has been, we believe, primarily on aprioristic grounds. In the long controversies of recent years regarding the interpretation of Castle's work the logical side of the case seems to have always been in the foreground. The same is the case when E. Baur calls our

<sup>2</sup> See pictures in *Jour. Exp. Zool.*, 22, 1917, pp. 614-15.

views in regard to the variability of the sex-factors *a priori* inadmissible. We believe that this intellectual attitude toward the problem is the result of Johannsen's doctrine of agnosticism in regard to the nature of the gene, which resulted in a kind of mystic reverence, abhorring the idea of earthly attributes for a gene. (Our distinguished opponents will excuse this somewhat extreme statement.) If, however, it can be proven that genes are substances with the attribute of definite mass, it would be illogical to deny their variability. Nobody will claim that a gene is a substance that passes unaltered from generation to generation. The elementary facts of development and regeneration show that this substance grows, at least, and increases in quantity. If, now, the substantial basis of heredity in the sex-cells is established by the assembling of all the factor-substances in their characteristic quality *and their correct quantity*, the situation is the same for the gene as for any other organic process: the varying conditions of the surroundings of the gene cause a certain amount of fluctuation in its quantity. This conclusion entirely changes the logical aspect of the question, whether or not a change of the gene by selection of variants is possible.

The strongest point of the anti-selectionists was that it is absurd to assume that a selection of somatic fluctuation has anything to do with the characters of the germ-plasm. With the quantitative view, however, which we believe to have proven in two elaborate cases, this situation changes. The somatic character in question, say amount of pigmentation, can only change toward a plus or minus side. This change is caused directly by a difference in the velocity of the reaction of some metabolic process which results in the deposition of pigment. Such a change of velocity of reaction, however, can be produced either by the action of the medium, and then it is a modification, or by fluctuation in the quantity of the gene, causing increase or decrease in the velocity. The resulting variation is of course, phenotypically, the same. Selection, therefore,

may be ineffective, if a modification only is selected; it will be partly successful if a combination of plus-quantity with plus-modification is selected; and fully successful if the exclusive result of plus-quantity of the gene is selected. The *deus ex machina* modifying factor, which, moreover, does not fit the decisive genetic facts in the most discussed case of Castle's rats nor our cases, thus becomes superfluous.

It is, moreover, perfectly logical to assume that selection of either plus or minus quantities of the genes changes the mode of the fluctuation of this quantity correspondingly in the succeeding generation. If the different quantities of the substances, which constitute the systems of multiple allelomorphs, are inherited, then every other quantity is also inherited. If the presence of the quantity *p* in the germ cells of the parents causes the reappearance of the quantity *p* in the germ cells of the children, the same fact applies to the quantities *q*, *r*, *s*—to every quantity which is present or has been selected. Selection can, therefore, change the quantity of the gene, and also, therefore, the somatic characters caused by quantitative differences in the gene, until the physiological limit is reached. This limit may be the limit for the character in question—for example, no pigment, self-color—or it may be the limit set by the necessary coordination of developmental processes. For example, in the development of a moth a certain gene causes, at a certain moment—during pupation—the evagination of the imaginal disks of the antenna. The correct quantity of the gene causes this process to take place at the correct time. A quantitative variation of the gene would cause the evagination to take place at the wrong time. We have, indeed, had strains of caterpillars where in many individuals this process took place in the last stage of the caterpillar, giving caterpillars with pupal antennæ. The quantity of the gene in question was in these cases not coordinated with the other genes and the action was produced too early. It is evident that quantitative changes

of this kind will lead to physiological impossibilities, monsters, etc. Here, then, is again the limit for selection of factorial quantities. It need hardly be added that such selection is necessarily orthogenetic.

Our own experiments in this line are, as far as they go at present, in perfect accord with Castle's work. We have, moreover, applied another type of experimental test, namely, selection in  $F_1$ . If a given pair of multiple allelomorphs differs in regard to the quantity of the factorial substance and this quantity is subject to fluctuation around a mean, the variability of the character in  $F_1$  is caused by the usual agencies producing fluctuations as well as by the different combinations of the parental quantitative values. Selection in  $F_1$  ought, therefore, to influence the curve in  $F_2$  in a certain number of cases, namely, when the plus or minus individuals are genetically plus or minus. Within the normal segregation of light and dark individuals in the 3:1 ratio a shifting of the mean for lightness and darkness must take place. In a series of such experiments we had a number of positive results. The following Table VIII may serve as an example:

TABLE VIII  
 $F_2$  WITH SELECTION IN  $F_1$  FROM CROSS  $K \times S$

	In Third Stage									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Plus selection .....	25.5	..	..	7.3	12.7	9.1	30	15.4	..	..
Minus selection.....	25	5.7	26.9	15.5	17.2	3.2	6.5	..	..	..

We believe that these facts and interpretations have a definite bearing on the problem of evolution. The first step in the differentiation of species which occurs in nature seems to be the formation of geographic races. The entire bulk of modern evidence in ecology tends to show the existence of clearly defined local forms for very restricted areas. For example, the ichthyologists differentiate forms of Salmonids and Coregonids for practically every river and lake; in the same way in the lower

organisms, like Daphnids and Rotatoria, different forms appear in different regions. The ornithologists describe different races for every river basin of the affluents of the Amazonas; the mammalogists do exactly the same thing for every area which was thoroughly covered. Where breeding experiments have been carried on it has been shown that the geographic races may be perfectly fertile with each other and may produce fertile offspring. In some cases, however, the transitional stages toward sterility are found. Thus the production of intersexual moths in crossing geographic races can be regarded as a step toward increasing incompatibility, which in one of the crosses attempted by us was an absolute one. In other cases only a small percentage of the offspring of the hybrids could be reared, as in the crosses of the North and South European *Callimorpha dominula*. We, therefore, with many evolutionists, feel convinced that the geographic races are the most important visible steps in species-formation in nature.

If we now look into the characters distinguishing geographic races, we very often find certain qualitative differences most conspicuous, for example, exchange of red and yellow color in the moths. A close study of definite examples, however, reveals that these differences are often more conspicuous than important. This is shown by the only group of information in the animal kingdom which we have both by ecological and genetic work—the geographic variation of land snails. The facts about the extreme variability of *Helix*, *Achatinella*, *Partula*, etc., are well known, as well as the irregularities in the confinement of definite types to definite localities. We have been so fortunate as to gain some insight into these facts through a very interesting collection which Dr. Haniel made in Timor and studied under our direction (not yet published). It was evident here, as in the other cases, that a series of unit factors for number, color, form of bands and ground color, which recombined freely, was involved. And practically all the combinations could be

reduced to the genetic factors which Lang worked out for *Helix*. But, exactly as in the classic cases, there was no possibility of stating a definite relation of these factors to the grouping according to localities. In some localities certain factors or combinations did not occur, but the attempt to classify the material along this line proved a failure. However, every group from each locality exhibited beside these factorial recombinations certain quantitative characteristics of size, proportions, etc., of the shell which were characteristic for definite localities. These, however, are the characters which probably fall in line with those caused by the quantity of the genes.

The difficulties which the facts of geographic variation create for the conception of species-formation by selection have often been discussed. Bateson in particular ("Problems of Genetics") scrutinizes them from the modern genetic point of view. They are indeed insuperable if all characters which show variations and recombinations are considered from this point of view. The extreme irregularity, for example, of the local combinations of types of shells in *Helix*, *Partula* and *Achatinella* makes it impossible to regard them as local adaptations. This is certainly true, but may be without any bearing on the species question at all. The factors and recombinations occurring in *Helix*, *Achatinella* and *Prodromus* are more or less the same, just as are the recombinations of coat colors in different rodents. They constitute a set of mutations and their recombinations which are proper to the type of germ-plasm of the group. They occur, recombine or fail to appear as chance wills, and seem to have no special selective value. We do not think that these are the characters which play a part in the evolution of species; they are, in most cases, independent of adaptation.

There are, however, reasons for supposing that such differences of characters as are based on the quantitative differences of the gene are those which are influenced by selection and are important for the formation of the first



steps toward diversification of species. We base this opinion on the following facts:

One of the few cases where selection in nature has apparently been seen at work under our eyes is the much-quoted case of melanic moths. We started in 1908 to work out the case of the nun, *Lymantria monacha*. The dark varieties of this moth have been known as rare occurrences for over a century. But only during the last decades have they spread and almost replaced the white forms. The analysis of the genetics of this case shows that the dark form is a dominant mutation to the white and that the many different stages of darkness, which form a complete series from white to black, are produced by sex-linked multiple allelomorphs. (Unfortunately, the interesting details can not be given at present.) How is it, now, that these combinations have come to replace the original form? Many hypotheses, some of them very strange, have been put forward; but it seems to us that the case is comparatively simple. The dark forms are stronger, more lively, better fliers, as far as we can tell from our experience with the animals in captivity. They are also larger (see Fig. 102, p. 267, in our "Einführung in die Vererbungswissenschaft," 2d ed., 1913). The melanism is in this case, therefore, only the most conspicuous superficial feature of a quantitative and progressive change in a gene which causes a definite metabolic condition, resulting in hardness as well as in the deposition of more pigment in the wings. The quantitative change has here a superficial expression and is therefore easily recognizable. But this visible pigmentation is not the really important character. How is it, then, that these melanic forms, and other forms in similar manner, have established themselves so suddenly? We may venture to point to the facts that the selection, as has often been stated, has occurred especially near the larger cities, and that the period during which this selection has taken place is the period of industrial development, *i. e.*, of restriction of forested areas near the cities. It is,



furthermore, the period of scientific and intense forestry and of economic entomology. Here we have the probable agencies that made life difficult for the moth and gave a great selective value to that advance in hardness which lies behind the melanic appearance.

We should point out here the difficulties which arise in the criticism of definite views of evolution on the basis of facts not analyzed genetically. The selective value of a climatic character may often be doubted on the ground that the same type occurs in a very different area admixed with the local form. But genetic analysis may often show that what appears to be the same type is in reality a different thing. The north European Arctiid, *Callimorpha dominula*, has wings marked with red; the Italian form has wings marked with yellow. In certain localities (one of them near Berlin) a yellow sport of the red form regularly appears, apparently the same form as the Italian one. We, as well as others, have crossed these forms. The yellow sport is a simple recessive to red and segregation occurs in the 3:1 ratio. The Italian yellow form, however—at least the ones from the Abruzzi, which we used—crossed with the red northern form, produces intermediate orange in  $F_1$  and in  $F_2$  every shade from red to yellow. The two yellows, which look alike and probably are chemically alike, are nevertheless products of a different metabolic process. In the sport the same metabolic process which usually leads to red pigment is changed by mutation only to the extent of the color change in the end-product. In the southern form a different type of metabolism results in the formation of yellow pigment, and the cross is therefore an entirely different cross, with different results.<sup>3</sup> As a matter of fact, the latter cross shows very much diminished fertility, as Standfuss has already pointed out. This shows how unsafe the ground is on which criticism of evolutionary questions without genetic test is based. That our example is not an exception is proved by the fact that Standfuss long ago formu-

<sup>3</sup> We may point out that herefrom a rational interpretation of dominance and blending can be derived.

lated the rule, that when two forms coexist in the same locality and are able to interbreed, they do not produce intermediates; but when the forms are geographically separated as local races, crosses between them result in a series of intermediates. Bateson says: "In this aphorism there is a good deal of truth." We think that the rule expresses the difference between a non-adaptational chance mutation and the adaptational change in the factorial quantities which may lead to a similar-looking, but physiologically different character. This character, although, like the non-adaptational one, is itself of no selective value, is the result of a general physiological change which does have a selective value.

This will become still more evident if we return once more to the study of the gypsy-moth. In studying the relations of the different geographic races as characterized by the multiple-allelomorphic characters in question, we find that these characters are paralleled closely by differences in the life-cycles. Without going into details, we may state as a fairly general rule that the races with high degrees of pigmentation in the later stages are the ones which show a fast development, comparatively short larval life and a long period of hibernation. The light races have a comparatively long larval period and a correspondingly short period of hibernation. The former races, furthermore, inhabit the areas where a long and cold winter occurs, while the latter are endemic in places which have a hot summer, early spring and mild winter. One might think that these different characteristics were simply the direct effect of temperature conditions. But that this is not the case is shown by the constancy of the differences when the races are bred in a different climate and also by experiments on the physiology of hibernation, which have convinced us that the time relations of the life-cycle are—of course, within the limits of fluctuation—a heritable trait of rhythmic character. These facts show where the adaptational character of the differences of the geographic races lies: the adaptation which fits the differ-

ent milieus is the life-cycle (in a broad sense). The visible distinctive characters of the races—aside from additional mutations of a non-selective nature—are nothing but the products of reaction of different types of metabolism, allied with the different time relations of the cycle. The method of the formation of geographic races in this case must, therefore, be the following. The first conquest of a new territory is of course only possible when the animal is preadapted, along general lines, to the new medium. But that it can maintain itself depends upon its power of special adaptation. The gypsy-moth, for example, has repeatedly been brought into England, but it has never established itself there. In the case of this form the special adaptation means the coincidence, in the first place, of the life-cycle with the seasonal cycle in nature. And it is here that all the discriminating effect of selection comes in. The quantitative changes of the genes which cause the time relations of the cycle are then the material for selection, and selection acts according to Darwinian principles until the equilibrium is established. Thus the genetic study of the quantitative changes of the gene reveals anew the truth of Darwin's conception. Furthermore, we see here how sterility of hybrids or complete incompatibility of new forms may arise. We have proved that the quantitative differences of the sex-factors, which are themselves nothing but adaptations to the time-relations of the cycle, are among the characteristic differences of these races.<sup>4</sup> There are, moreover, responsible for the incompatibility in regard to sex which results in intersexuality after crossing. Changes of exactly the same type may easily make any cross-breeding impossible, since no organism can develop unless all the processes of differentiation are coordinated in respect to their velocity. Here we see, finally, why geographical races are so often uniform and are characterized by certain traits of

<sup>4</sup> Compare also Pflüger's and R. Hertwig's work with frogs and Cuénot's with starfish, demonstrating similar facts in regard to geographic variation of sexuality.

a quantitative character even when additional mutations and their recombinations make them at first sight appear diversified. This uniformity indicates the adaptational type produced by selection of the quantitative variations of some vital gene; the differences are only a difference in apparel.

In conclusion, we may point out three groups of facts which, of the greatest importance for evolution, have always been a hard nut for the mutationists to crack. The first is the series of temperature-experiments in *Lepidoptera*—and similar experiments in *Amphibia*, *Crustacea*, etc.—that lead to the production of aberrant forms which resemble closely certain geographic varieties. But, with the exception of certain often-quoted cases, these aberrations are not hereditary. In the light of our experiments these facts are not surprising. The effect of the temperature experiments is to change the normal time-curve of certain metabolic processes. The effect is, therefore, due to this change of one of the variables of the reactions in question. The quantitative change of the substance of a gene, however, which we found to be at the basis of the geographical variations, also produces a difference in respect to the time-curve and therefore the same effect, this time a heritable effect. If we now select the plus individuals in this type of experiment—and this applies to all analogous experiments—we may simply select a modification. But we also may select the combination of a plus-modification with a plus quantity of the gene in question. If the experiment is repeated, the next generation will then show a still stronger reaction, or, if the experimental influence is not repeated, there will be an after effect of the experiment on the parents. It is remarkable that such results, which were to have proved the inheritance of acquired characters, always turned out, when characters relating generally to the life-cycle were in question, characters which also appear in the geographic races of the form. Extreme mutationists used to deny or disregard these facts. Here we have a simple

explanation for them which both does justice to the facts themselves and falls in line with modern genetic views.

Furthermore, we now see the exact meaning of Darwin's view, which he had to express in a somewhat ambiguous way on account of the lack of experimental data which would have permitted clearer expression. His essay of 1842, the forerunner of the "*Origin of Species*," begins with the words: "An individual organism placed under new conditions sometimes varies in a small degree and in very trifling respects, such as stature, fatness, sometimes color, health, habits in animals and probably disposition. . . . Most of these slight variations tend to become hereditary." This statement shows clearly what Darwin had in mind. If he assumes that some variations, which are produced by change of conditions, are sometimes non-heritable, but tend to be inherited, we can now explain what this means. The variations which, as geographic races, form the first steps in the formation of new species are indeed exactly the same whether or not they are inherited. Their direct physiological cause is also identical, being a change in the rate of a definite process during differentiation. Only the ultimate cause is different; in the one case the original quantity of the gene determines the rate of differentiation—which then is hereditary—from the beginning; in the other case an outside factor is active, retards or accelerates the same reaction to the same degree. With this additional bit of interpretation, Darwin is right, after all.

The other group of facts includes certain details of mimicry (mimetism). We believe that the general principle of mimetism has been fully explained genetically by Punnett. But there are certain details which his selectionist opponents point out which constitute strong evidence against Punnett's view. We think that the most valid argument against the Mendelian view of mimetism has been derived from the facts about the parallel geographic variation of model and mimic. If our genetic conception of geographic variation is correct, this point

is not difficult to understand. If the resemblance of model and mimic is based on the presence of similar chance- or non-chance combinations of genetic factors, and if geographic variation consists in the specific adaptation of the quantity of certain genes to a required velocity of some vital reaction, it is very natural that similar genes in model and mimic should be in exactly the same situation and should undergo parallel changes.

The third important set of facts to be considered is the problem of domestication. Darwin's view is well known, as well as the solution of a great part of the problem through Mendelism. The latter shows that selection of the recombinations after cross-breeding (besides picking of mutations) is the chief source of success in domestication. (See our demonstration of this fact regarding the improvement of pigs in "Einführung in die Vererbungs-wissenschaft," 2d ed., 1913, pp. 276-80.) That this fact was well known to Darwin is shown, for example, in his report about Lord Orford's greyhounds ("Variation of Animals," etc., Ch. 1). But he believed, in addition, in a positive effect of selection of small variations. Wherever he tabulates such characters, most or all of them are quantitative characters of a kind which we can assume to be dependent upon the presence of definite quantities of a gene. Here we may have the solution of the difficulties which the problem of domestication affords in spite of mutation and recombination. No doubt the high capacity for fattening was crossed into our hogs with Asiatic forms. But selection of plus-quantities of the responsible gene enabled us to obtain the character as it stands to-day.

OSBORN ZOOLOGICAL LABORATORY,  
YALE UNIVERSITY,  
NEW HAVEN, CONN.

## MATERNAL INHERITANCE IN THE SOY BEAN

H. TERA0

THE IMPERIAL AGRICULTURAL EXPERIMENT STATION, TOKYO, JAPAN

THE soy bean, *Glycine hispida* Maxim., shows as different types two cotyledon colors, yellow and green. The beans with yellow cotyledons have two types of seed-coat colors, namely, green and yellow, while the beans with green cotyledons have always green seed-coats.<sup>1</sup> The inheritance of these types of cotyledons and of seed-coats has been proved by the author's experiments to be maternal. A brief notice of the experiments will be given in the following.

The green and yellow colors of cotyledons and seed-coats are obviously attributed to chlorophyll, which, on the ripening of the beans, is either changed from green into yellow or remains green. Further, according to the author's observations, the chlorophyll in the vegetative parts of the plant shows the same behavior as the chlorophyll of the cotyledons; in other words, the leaves and stems of the varieties with yellow cotyledons turn to a yellow color when they are gradually dying coincident with the ripening of the beans, while those of the varieties with green cotyledons remain green sometime after the dying of the whole plant. These facts suggest that the two types of cotyledon colors may represent two kinds of chlorophyll, one which changes into yellow under certain physiological conditions and one which is not so affected. The chlorophyll of the seed-coats, however, seems to behave somewhat differently from the chlorophyll in all

<sup>1</sup> Black and brown pigments also appear in the seed-coats of certain varieties. These pigments are entirely independent of the green and yellow colors here referred to in their inheritance, but they make the latter colors invisible or at least indistinct. By proper crosses, however, one can test whether a seed-coat covered by the black or brown pigment belongs to the green or the yellow category.

TABLE I  
SOY BEAN CROSSES MADE IN STUDYING THE INHERITANCE OF GREEN AND YELLOW COLORS OF COTYLEDONS AND OF SEED-COATS

	Crossing No. I		Crossing No. II		Crossing No. III		Crossing No. IV		Crossing No. V		Crossing No. VI	
	Cotyle- dons	Seed- coat	Cotyle- dons	Seed- coat	Cotyle- dons	Seed- coat	Cotyle- dons	Seed- coat	Cotyle- dons	Seed- coat	Cotyle- dons	Seed- coat
Parents												
Female . . . . .	green	green	green	green	yellow	green	yellow	green	yellow	green	yellow	green
Male . . . . .	yellow	yellow	yellow	green	green	green	green	yellow	yellow	yellow	yellow	yellow
F <sub>1</sub> -Ind. . . . .	green	green	green	green	yellow	green	yellow	green	yellow	green	yellow	green
No. Ind. . . . .	24	24	3	3	40	40	4	4	9	5	5	5
F <sub>2</sub> -Ind. . . . .	green	green	green	green	green	yellow	green	green	green	yellow	yellow	green
No. Ind. . . . .	3,129	1,248	322	216	825 : 288 (74.1% : 25.9%)	846	436	418 : 128 (76.6% : 23.4%)	1,815	169	56 : 19 (74.7% : 25.3%)	56 : 19 (74.7% : 25.3%)
F <sub>2</sub> -Fam. . . . .	green- constant	green- constant	green- constant		yellow- constant	yellow- constant	yellow- constant	yellow- constant	yellow- constant	yellow- constant	yellow- constant	yellow- constant
No. Fam. . . . .	1,248	216	216		1,113	436	436		546	74	74	
No. Ind. . . . .	72,501	16,498	16,498		28,231	2,341	2,341		55,354	4,635	4,635	



other parts of the plant, since, as was already noted, yellow cotyledons are accompanied by green seed-coats in certain varieties.

The crossing experiments which have been made by the author since 1910 with these different types of beans have produced the results shown in Table I, the main facts being summarized as follows.

I. The  $F_1$  cotyledons of the crosses reciprocal to each other are of the same character as the female parents. In respect to the cotyledon colors, the  $F_2$  and following generations show the characters of the  $F_1$  generation exclusively, instead of a Mendelian segregation between the yellow and green colors. Hence we are probably dealing with characters which can be inherited only through the female parents.

II. The inheritance of the seed-coat colors is a more complicated phenomenon. In the cross "green cotyledons, green seed-coat" ( $\text{♀}$ )  $\times$  "yellow cotyledons, yellow seed-coat" ( $\text{♂}$ ), the green seed-coat is inherited through the female parent exclusively, just as in the case of the cotyledon colors; but in the reciprocal cross the green and yellow seed-coats show Mendelian segregation, the former being dominant.

The maternal inheritance observed above was not due to self-fertilization succeeding failures in artificial crossing, because several other characters showed inheritance through the male parents.

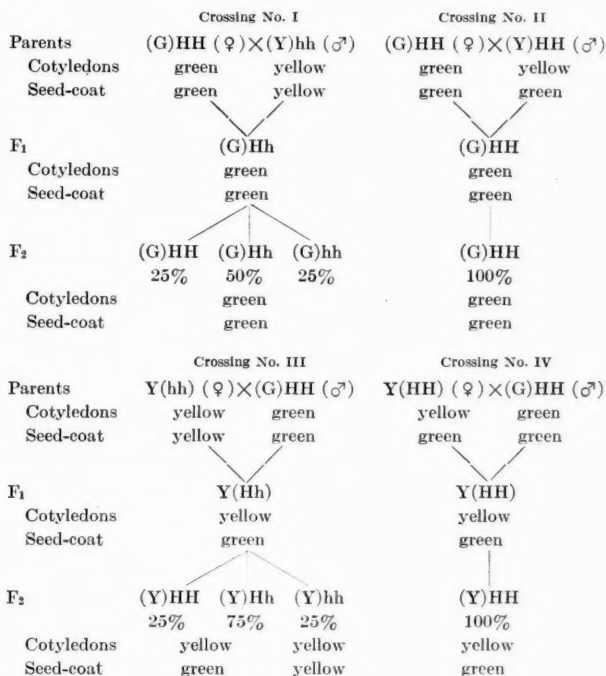
An interpretation of the inheritance phenomena under consideration is suggested as follows. In the first place, let us refer again to the two different kinds of chlorophyll assumed to be concerned in producing the green and yellow cotyledons; namely, the chlorophyll which can be changed into yellow and the chlorophyll which remains green. (These will be denoted respectively as "(Y)" and "(G)" in the later descriptions.) These characteristics of chlorophyll may be due to heritable traits of the chromatophores or of the cytoplasm, and not to hereditary elements in the nucleus. As, on the fertilization of

the egg-cell, the chromatophores and the cytoplasm of the female gamete will probably remain as such without being supplemented by those from the male gamete, their characteristics would naturally be inherited only through the female parent. In the second place we may assume that a pair of Mendelian factors is concerned in the inheritance of the colors of the seed-coats. The factor "H" inhibits the chlorophyll "(Y)" in the seed-coat of the beans with yellow cotyledons from changing to yellow, producing beans with yellow cotyledons and green seed-coat; the absence of the factor "H," expressed by "h," allows the seed-coat of the bean with yellow cotyledons to remain yellow. The seed-coat of the bean with green cotyledons remains green no matter whether the factor "H" is present or absent, because the beans of this kind have the chlorophyll "(G)" which is incapable of changing the color.

The justice of the contention regarding the bean with green cotyledons, moreover, is supported by the following observations. The  $F_2$  families of the crosses "green cotyledons, green seed-coat" ( $\text{♀}$ )  $\times$  "yellow cotyledons, yellow seed-coat" ( $\text{♂}$ ) were actually composed of two kinds of individuals which were distinguishable from each other by a slight difference of the intensity of green color in the seed-coats, and the numerical relation between these two kinds of individuals was approximately the Mendelian mono-hybridal segregation ratio, the darker seed-coat being dominant to the lighter one. Again, in the  $F_3$  generation of these crosses, there were obtained three types of families, two which were uniformly of the darker and of the lighter seed-coats respectively and one which was a mixture of both. By comparing the green seed-coats of the female parents in these crosses with those of the progeny, the former was found to belong to the darker class mentioned above. These variations in the green color of the seed-coats may be regarded as being due to the influence of the Mendelian factors "H" and "h" respectively on the chlorophyll "(G)"; from which it follows

that the method of inheritance in the beans with yellow cotyledons obtains also in the beans with green cotyledons.

Keeping these statements in mind the cases in Table I may be illustrated as follows:



If the foregoing interpretation really represents the facts in this investigation, we may consider also crosses in which forms such as (G)Hh, (G)hh, and (Y)Hh were used as the parents, since in these crossings phenomena different from those in Table I would be expected. These expectations have been fulfilled in further experiments in which individuals from the previous experiments representing different intensities of seed-coat color were used as the parent plants. The results of these crosses, accompanied by interpretations, are shown in Table II.

TABLE II

CROSSES MADE AMONG THE PROGENY OF THE HYBRIDS SHOWN IN TABLE I

		Parents		F <sub>1</sub>		F <sub>2</sub>	
		Female	Male	Character	No. of Individuals	Character	No. of Individuals
Crossing No. VII . . . . .	Cotyledons	yellow	green	yellow	22	yellow	2,381
	Seed-coat	yellow	green	yellow	22		
	Interpret.	(Y) hh	(G) hh	(Y) hh	100%		
Crossing No. VIII . . . . .	Cotyledons	yellow	green	yellow	18	yellow	1,963
	Seed-coat	green	green	{ green	10		
				{ yellow	8		
	Interpret.	(Y) Hh	(G) hh	{ (Y) Hh	50%		
				{ (Y) hh	50%		
Crossing No. IX . . . . .	Cotyledons	yellow	green	yellow	9	yellow	1,108
	Seed-coat	green	green	{ green	7		
				{ yellow	2		
				{ (Y) HH	25%		
	Interpret.	(Y) Hh	(G) Hh	{ (Y) Hh	50%		
				{ (Y) hh	25%		

The maternal inheritance described in this paper seems to be essentially the same phenomenon as the inheritance of the character "*albo-maculata*" which was studied by Correns<sup>2</sup> in *Mirabilis Jalapa* and also by Baur<sup>3</sup> in *Antirrhinum majus*. In each case one is dealing with chromathophore characters.

HARVARD UNIVERSITY, BUSSEY INSTITUTION,

<sup>2</sup> Correns, C., *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Bd. I, 1909, pp. 291-329; *Ibid.*, Bd. II, 1909, pp. 331-340.

<sup>3</sup> Baur, E., *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Bd. IV, 1910, pp. 81-102.

## SHORTER ARTICLES AND DISCUSSION

### LINKAGE IN MAIZE: THE *C* ALEURONE FACTOR AND WAXY ENDOSPERM<sup>1</sup>

IN 1912 Collins<sup>2</sup> presented data which showed a linkage between waxy endosperm and aleurone color in certain hybrids of Chinese and American corn. A summary of the  $F_2$  data in Table II, p. 579,<sup>2</sup> gives the coefficient of association as .821. This is equivalent, approximately, to a 3.5-1 gametic ratio, and a crossing-over percentage of 22. The percentage of waxy grains is about 21 and colorless about 25. This is good evidence that Collins is dealing with material heterozygous for waxy endosperm and heterozygous for only one factor in aleurone. In the back cross data in Collins's Table IV none of the ears shows the 1:1 relation between colored and colorless expected from plants heterozygous for one color factor. The material in that table apparently involves more than one aleurone factor in the heterozygous condition and before such data may be considered in any linkage study they must be corrected for this or the true values for the percentage of crossing over can not be ascertained. The coefficient of association need not be used if we are dealing with back cross data. If it seems desirable to use the coefficient of association with this sort of data new tables should be calculated from the gametic series  $n:1:1:n$  corrected for the respective aleurone factor conditions.

The advantage of back cross data is obvious. Data of this nature obtained by the writer from crosses of plants heterozygous for one aleurone factor and for waxiness with double recessive plants are presented in the table on p. 58.

Families 6, 99, and 100 are derived from colored corneous seeds heterozygous for aleurone and waxiness. Families 9 and 101 are colorless waxy plants. The first nine ears give an average crossing over of 26.7 per cent. or a gametic ratio of 2.75:1. Ears 8 and 9 show repulsion instead of coupling, but this does not

<sup>1</sup> Paper No. 66, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

<sup>2</sup> "Gametic Coupling as a Cause of Correlations," AMER. NAT., 46, pp. 569-590. 1912.

necessitate a separate summary for the crossover and non-crossover classes of the coupling and repulsion families. The deviations from the average are more than twice the probable error in ears 1, 3, 4, and 9, between one and two times in ears 5 and 7, and less than the probable error in ears 2, 6, and 8.

BACK CROSS DATA: HETEROZYGOUS CORNEOUS COLORED  $\times$  WAXY COLORLESS

Ear Number	Parentage	Corneous Colored	Corneous Colorless	Waxy Colored	Waxy Colorless	Non-Cross-overs to Cross-overs	Per Cent. of Crossing Over	Deviation from 26.7 Per Cent.	Probable Error in Per Cent.	Dev. P.D.	Per Cent. Waxy	Per Cent. Colorless
1	100(6) $\times$ 101(1)	147	58	65	133	280:123	30.5	3.8	1.49	2.55	49.1	47.4
2	100(1) $\times$ 101(3)	104	24	32	67	171: 56	24.7	2.0	1.98	1.01	43.6	40.1
3	101(9) $\times$ 100(9)	102	60	43	137	239:103	30.1	3.4	1.61	2.11	52.6	57.6
4	100(5) $\times$ 101(4)	170	49	39	136	306: 88	22.3	4.4	1.50	2.93	44.4	47.0
5	101(3) $\times$ 100(8)	124	53	60	153	277:113	29.0	2.3	1.51	1.52	54.6	52.8
6	101(5) $\times$ 100(6)	71	24	9	31	102: 33	24.4	2.3	2.57	.89	29.6	40.7
7	100(11) $\times$ 101(4)	140	42	63	124	264:105	28.5	1.8	1.55	1.16	50.7	45.0
8	101 (2) $\times$ 99(1)	46	111	103	32	214: 78	26.7	0	1.75	.00	46.2	49.0
9	99 (1) $\times$ 101(9)	69	229	195	60	424:129	23.3	3.4	1.27	2.68	46.1	52.3
	Total					2,277:828	26.7		0.54		47.7	48.4
	6 (6) $\times$ 9(6)	118	114	128	131	249:242	49.3	22.6	1.35	16.74	52.7	49.9

Owing, perhaps, to the difficulty in separating waxy from corneous grains the percentage of waxy grains for the total of the 9 ears is only  $47.7 \pm .6$ . The deviation from the expected 50 per cent. is nearly four times the probable error, indicating a poor fit. The percentage of colorless grains is 48.4 and the deviation is two and two thirds times the probable error. Here the separation is accomplished with a somewhat greater degree of accuracy. On the whole, the data seem to show conclusively that we are dealing with a linkage between waxy endosperm and one of the aleurone factors.

Ear No. 10, which is derived from a non-linkage family and included in the table for comparison with the first nine ears, is also the result of a back cross. The per cent. of crossing over is 49.3, which is practically equivalent to independent inheritance. The deviation from 26.7 per cent. of crossing over is 16.74 times the probable error and the odds against this being due to random sampling are enormous.

EVIDENCE THAT THE *C* FACTOR FOR ALEURONE COLOR IS CONCERNED

Although the linkage data are interesting and valuable, it is perhaps of greater interest and value in the study of maize in-

heritance to know which of the aleurone factors is concerned in this linkage. This may be determined, where the inhibitory factor *I* is not concerned, by crossing plants grown from either colorless waxy or colorless corneous grains taken from families showing linkage with plants that are homozygous recessive in turn for one of the aleurone factors and homozygous dominant for the remaining factors. Plants of this nature were available in Professor Emerson's aleurone testers.

At least five factors are now known to be concerned with development of aleurone color. They are known as the *A*, *C*, *R*, *Pr* and *I* factors. *A*, *C* and *R* are necessary for the development of red. The dominant *Pr* factor changes red to purple. That the *Pr* factor is not concerned in this linkage is evident from the fact that the linkage relation is observed in segregations of colored and non-colored aleurone and waxy and corneous endosperm regardless of whether they are purple or red, and from the fact that only red aleurone seeds were used in obtaining the back cross data which show the linkage. That the inhibitor is not involved is inferred from the fact that the segregation on the original parent ear was 195 corneous colored, 95 corneous colorless, 95 waxy colored and 15 waxy colorless which is approximately a 3:1 segregation of colored to colorless aleurone. The relation of the *A*, *C* and *R* factors to waxy endosperm remains to be accounted for. This may be determined as stated above by the use of aleurone testers, which are named for the pair of factors which is homozygous recessive. The following diagram explains the method of testing for these factors.

Constitution of Aleurone Testers	The Constitution of Colorless Grains from the 3:1 Ear may be		
	<i>aaCCRR</i>	<i>AAccRR</i>	<i>AACCrr</i>
<i>A</i> tester, <i>aaCCRR</i> .....	No color	Color	Color
<i>C</i> tester, <i>AAccRR</i> .....	Color	No color	Color
<i>R</i> tester, <i>AACCrr</i> .....	Color	Color	No color

If the *C* factor were linked with the factor for waxy endosperm no color should appear in the  $F_1$  from a cross between the *C* *R* and *A* testers colored ears should be obtained. Crosses of this nature were made in 1916 and 1917 with the following results:

COLORLESS ALEURONE WITH *C* TESTER

Year	Parentage	Approximate Number of Seeds	Color of Aleurone
1916.....	1 (2) $\times$ 6857 (9)	360	No color
1916.....	2 (14) $\times$ 6857 (12)	240	" "
1916.....	2 (9) $\times$ 6857 (4)	500	" "
1917.....	101 (1) $\times$ 7506 (2)	250	" "

COLORLESS ALEURONE WITH *R* TESTER

1916.....	1 (5) $\times$ 6867 (19)	480	Colored
1916.....	2 (1) $\times$ 6868 (6)	200	"

COLORLESS ALEURONE WITH *A* TESTER

1917.....	101 (7) $\times$ 7505 (2)	150	Colored
-----------	---------------------------	-----	---------

The above data are believed to show conclusively that the *C* factor for aleurone is linked with the factor for waxy endosperm, because the *R* and *A* testers caused the development of aleurone color when crossed with colorless individuals from the same family while the *C* tester did not.

## NON-LINKAGE OF ALEURONE COLOR AND WAXY ENDOSPERM

It is interesting to know that in ear 10, which shows no linkage, the *C* factor for aleurone was not heterozygous. A colorless waxy individual from this family crossed with the *C* tester produced an ear consisting of approximately 300 seeds, all of which showed colored aleurone.

Another waxy colorless individual of the same family crossed with the *R* tester produced an ear with 25 seeds, all of which were colored. Thus the *C* and *R* factors are eliminated with some degree of assurance. The *A* factor apparently is heterozygous in this family, but unfortunately the writer has obtained no crosses with the *A* tester to verify the conclusion reached by the process of elimination. This may be considered as indirect proof of the *C* factor as the aleurone factor which is linked with the waxy endosperm factor.

## SUMMARY

(a) Collins has presented conclusive evidence of the linkage between waxy endosperm and aleurone color. The writer has presented additional evidence from back crosses, which shows the



intensity of the linkage in the material at his disposal to be equivalent to 26.7 per cent. of crossing over.

(b) It has been shown directly, by means of crosses between colorless individuals in a linkage family and aleurone testers and indirectly by means of aleurone tests with a non-linkage family where the *A* factor and not the *C* factor is heterozygous, that the *C* factor for aleurone is linked with the factor for waxy endosperm.

T. BREGGER

CORNELL UNIVERSITY

### INHERITANCE IN ORTHOPTERA

In a recent paper (Nabours, '17) Nabours has continued his admirable studies of inheritance in *Paratettix*. The paper is backed up with an abundance of data, from which a number of facts are deduced. In his discussion, he attacks certain modern hypotheses, and since it appears to me that his strictures are not entirely justified, I venture here to review the evidence, and make certain comments on it.

The following facts, several of which were well brought out in a previous paper (Nabours, '14), are presented:

1. A large number of distinct, true-breeding forms of *Paratettix* occur "in nature." Of these he has collected at least fourteen or fifteen. He no longer looks upon each as a distinct species, and he has dropped the "specific names" he suggested for them in the previous paper.

2. The distinguishing characteristics of these forms fall into two groups in their mode of inheritance: (a) Fourteen color patterns act as allelomorphs to each other. (b) A fifteenth pattern is "allelomorphic only to its absence."

3. One of the characters of the "multiple allelomorph" group does not always act as an allelomorph to the other members of the group. This is the character I of his first paper, which was noted then for the same behavior. Rather, it behaves (to put it briefly, but in words very different from Nabours's) as if it were closely but not completely linked to the others.

Because I wrote a review of Nabours's first paper on this subject (Dexter, '14), I feel a certain responsibility for what I think are mistaken viewpoints concerning the multiple-allelomorphic nature of this group.

Bellamy, working in the same laboratory, contributes also an excellent study on the same subject, but based on a different genus of *Tetriginae* (Bellamy, '17). Both he and Nabours have apparently accepted as proven that there is here a large group of determiners allelomorphic to each other, and I am quoted in support of this idea. Inasmuch, however, as I made certain reservations which are important in the light of the new data presented, I beg to quote a portion of my former paper.

As Sturtevant has pointed out, for any case to which the idea of multiple allelomorphism is applicable, an equally valid explanation may be found in "complete linkage" of the factors concerned. To decide in any case between the two explanations would be impossible.

If however linkage were not complete, a "cross-over" class . . . might occur, and this would suffice to rule out the explanation based on multiple allelomorphs. Such a cross-over class perhaps is furnished by the BEI individual.

I then suggested that since the BEI individual had been lost before it could be tested, the cross be repeated, and said:

If then BEI forms should occur again, and in these, when mated to other forms, the factors B and I should be found to stay together to the same extent as before they separated, it would show that close linkage rather than multiple allelomorphism explains this particular instance.

Nabours has repeated this experiment, using the character S instead of E, and has again obtained such a cross-over, BIS. With this individual, he has carried out breeding tests.

Apparently forgetting what had been pointed out in my paper, he says:

The significant feature is the complete combination or linkage, apparently permanent, of the factor for S, and the factor for the modified I. . . This combination, IS, becomes a new form, *a new multiple allelomorph* (italics not original), pairing with and allelomorphic to any other multiple allelomorph with which it has been tried. . . It is not possible for me to suggest the means by which the combination or linkage was effected.

(One must protest against the use of words which permits a single determiner to be called a "multiple allelomorph.")

The answer that he was unable to give is obvious. Perhaps there are thirteen characters here whose determiners are allelomorphic to each other. That is possible, perhaps probable,

though unproved. But I is not a member of that group, but is only linked to it, being, as we may say, in the same chromosome. The work that Nabours has done makes that certain, and disposes also, by the way, of the likelihood that non-disjunction explains the similar case in the first paper (Bridges, '16).

Nabours has made a sort of mystery of the character called G in his first paper, but now called  $\theta$ , which, he says, is "only allelomorphie to its absence." Ignoring the philosophy of this statement, he has shown that  $\theta$  mendelizes independently of the other characters. He suggests that such determiners may be of frequent occurrence. He has shown that by substituting Greek letters for English letters the formulæ will work out as well as they did before, and has naïvely applied the method to the case of comb inheritance in poultry. His difficulty is simply caused, and Bellamy has pointed out its solution:

It need only be assumed that the determiner is borne by some other chromosome.

In *Drosophila* some four or five years ago, the determiner for bent wings was the only one known for the fourth chromosome group. If at that time we had known only one other set of characters in *Drosophila*, viz., that of the white-eosin group, the situation would have been parallel to the one described by Nabours. We might speak of a half dozen or so of "characters allelomorphie to each other," and of one, bent, "allelomorphie only to its absence." Later on, when we found other characters whose determiners were located in the fourth chromosome, we should modify our theory. Nabours's industry in his research makes me feel safe in prophesying that he will yet discover something linked to  $\theta$ .

He says parenthetically that two other characters "apparently of the nature of  $\theta$ " have been discovered. It is important to find out their linkage relations and we shall wait eagerly to hear of them. In the meantime we must conclude that he has discovered the beginning of at least two chromosome groups.

#### BIBLIOGRAPHY.

Bellamy, A. W.

1917. Studies of Inheritance and Evolution in Orthoptera, IV.  
*Journal of Genetics*, Vol. 7, p. 55.

Bridges, C. B.

1916. Non-Disjunction as a Proof of the Chromosome Theory of Heredity. *Genetics*, Vol. 1.

Dexter, J. S.

1917. Nabours's Breeding Experiments with Grasshoppers. *AMERICAN NATURALIST*, Vol. 48, p. 317.

Nabours, R. K.

1914. Studies of Inheritance and Evolution in Orthoptera. *Journal of Genetics*, Vol. 3, p. 141.  
1917. Studies of Inheritance and Evolution in Orthoptera, II and III. *Journal of Genetics*, pp. 1-54.

JOHN S. DEXTER

UNIVERSITY OF SASKATCHEWAN

